Correlated Responses to Selection for Wing Length in Allozyme Systems of Drosophila melanogaster

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Summary. Significant changes of genotypic structure in 20 lines selected for wing length are detected by analysis of the allelic frequencies of several enzyme loci (XDH, LAP-D, EST-6, 1-APH, ADH, α-GPDH). These changes are not haphazard but a consequence of the effects of selection on the genetic structure of the population, since replicate lines always behave in a parallel way. The changes are larger in the lines selected for short wings, in which the genetic variability decreases considerably. This decrease is the result of selection for homozygosity, detected at the allozyme loci, but most probably reflects homozygosity of more or less extended chromosomal segments. Selection for wing length, especially for short wings, favoured recombinants of the initial founder chromosomes. Only in the 1-APH and the EST-6 loci, separated by 11.7 centimorgans on the genetic map, do the alleles linked in the founder lines change in parallel in the control and long wing lines. The correlated response in the allozyme allele frequencies cannot be accounted for by a direct influence of the allozymes on the variability in wing length. The changes in the EST-6, 1-APH and perhaps in the LAP-D, can be explained by a direct effect of natural selection on the allozyme loci, probably in interaction with the effect of selection for wing length on linked loci. This last effect seems to be the main factor contributing to the change detected in the XDH locus.

Key words: Artificial selection — Selection for wing length — Correlated responses to selection — Allozyme systems — Drosophila melanogaster

Introduction

An enormous potential variability in genotypes controlling quantitative traits has been detected in artificial selection experiments. Classical examples of these experiments are those by Mather (1941), selecting on abdominal chaetae of Drosophila melanogaster, Robertson and Reeve (1952) and Reeve and Robertson (1953), on wing and thorax length of Drosophila melanogaster, and Falconer (1953), on body size in mice. Also, numerous changes in non-selected traits, accounted for by pleiotropy or by linkage of the genes controlling the selected characters, have been observed (Mather and Harrison 1949; Prevosti 1958). However, only guesses on the structure of the genotypes controlling these traits and on the relationships between these genotypes and the results obtained, are possible. This situation exists because of the general difficulties confronting the genetics of quantitative traits, arising from the complexity of the genotype controlling these traits and the difficulties in separating the component unit factors. Because of this, the results obtained in experiments with these traits are usually only open to statistical analysis at the phenotypical level, leading subsequently to conclusions about the genotype also only of a statistical nature. Frequently, several alternative models or situations fit these statistical results.

One attempt to go farther than statistical inferences on the genotype was the work by Prevosti (1967), on selection for wing length in Drosophila subobscura in which a control of the frequencies of chromosomal arrangements was carried out in the selected lines. Selection for long wings favoured heterozygous combinations for chromosomal arrangements, whereas selection for short wings generally fixed specific chromosomal arrangements in homozygous combination. These results were considered relevant for explaining the asymmetrical response obtained from the selection: selection for long wings is less effective in changing the mean of the population than selection for short wings.

The results of Lewontin and Hubby (1966) led to the knowledge of the existence of a great amount of genetic variability expressed in differences at the protein level, especially in allozyme systems, detectable with electrophoretic techniques. It is tempting to consider whether or
not this variability at least partially coincides with that found in quantitative traits. Thus, it appears as possibly rewarding to carry out artificial selection experiments in quantitative traits, determining at the same time the allelic frequencies in some polymorphic allozyme systems. Even if the allozyme loci are not physiologically related to the selected quantitative traits, these loci can serve as markers of chromosome segments furnishing information about the changes in the genotypic structure during selection.

Following this idea we planned selection experiments on wing length in *Drosophila melanogaster*, measuring at the same time the allelic frequencies in some allozyme systems. The purpose of these experiments was to obtain information at the single locus level, paralleling the data obtained at the level of supergenes in the above mentioned experiments by Prevosti. Some preliminary results have already been presented (Aguadé et al. 1973).

**Materials and Methods**

*Drosophila subobscura*, the species used by Prevosti (1967) for studying the relationships between selection for wing length and chromosomal arrangement frequencies, is not suited for our present purpose. Most individuals of this species are heterozygous for one or several chromosomal arrangements. This peculiarity results in limited recombination between the loci contained in the inversions responsible for the different arrangements or under their influence. This was the reason for choosing *Drosophila melanogaster* for our experiments. However, obtaining stocks of *Drosophila melanogaster*, from natural populations and thus free of variability in chromosomal arrangements, was not as easy as had been expected. The Spanish populations, from which some of the experimental stocks were extracted, have extensive variability in their chromosomal arrangements.

**Origin of the Stocks**

The purpose of these experiments is analytical. We search for information, as precisely as possible, on the effects of selection for a quantitative trait on the structure of the genotype. To obtain this, it is convenient to begin each selection line with the simplest and more definite structure possible: crossing two isogenic or inbred lines. When we cross two isogenic lines initially we have only two chromosomal types — and crossing-over between them is the origin of all the new chromosomes present in successive generations. In crossing inbred lines we have an approximation to this situation.

This known and definite structure of the founder populations better suits the purpose of the present paper than the foundation of populations with a random sample of chromosomes of unknown constitution, which would be more suitable for experiments with other purposes, i.e. trying to simulate natural populations in population cages. Another point of uncertainty that we eliminate by crossing two isogenic or inbred stocks for the foundation of the selection lines, is the possibility of confusing more than one allele within the same electrophoretic mobility. The problem of linkage disequilibrium with other genes would be reduced if a parallel tendency was observed when selecting several populations with different pairs of starting chromosomes.

Table 1 contains the origins and genetic constitutions of the lines used in the foundation of the 5 populations analysed. All lines used were tested cytologically for the absence of inversions. Normal levels of recombination along the whole third chromosome were also found when making the adequate crosses with a multiple marker stock for that chromosome (yu cu ce). From each population two replicated lines were selected for long wings, two were selected for short wings, and one control was established. These lines, as well as the designation used thereafter for them, are also found in Table 5.

In the 5 populations, both founding stocks were crossed, resulting in a founding population with frequencies \( p = q = 0.5 \) for each allele in each locus, with the exception of the fifth population, in which the i-APH locus had a frequency of 0.74 for the fast allele and 0.26 for the slow allele. The experiments were planned to study the four allozyme loci indicated in Table 1, however some data about other loci have been collected for the LX2 and the LXEP lines. The alcohol dehydrogenases (ADH) and \( \alpha \)-glycerophosphate dehydrogenases (\( \alpha \)-GPDH) have been analysed in the 0 and last (9th) generations of the LX2 lines. The \( \alpha \)-GPDH has also been analysed in the 0, 3 and last (6th) generations of the LXEP lines. As one of the foundation stocks (3009 from Umed) of the lines LX1 and LXEP was homozygous for the visible mutant ebony these lines had the initial frequencies \( e^* = 0.5 \) and \( e = 0.5 \). This offered the possibility to measure the changes in the frequencies of the alleles, which has been done in the LXEP lines.

**Selection Method**

Five vials containing 100 eggs each, were cultivated every generation in the selected lines. After complete emergence of the adults, 20 dd and 20 virgin \( 99 \) were randomly sampled, from each of these vials and measured. The 4 individuals of each sex, from each vial, with the longest or shortest wings were selected. So, a total of 20 couples among 100 measured ones were put together and after mating, their eggs were collected in order to obtain the next generation. The control lines were maintained with 15 vials per generation. Samples of 100 individuals, corresponding to 200 alleles for each locus.

**Electrophoretic Technique**

The electrophoretic analysis of the LAP-D locus was carried out using the technique of Beckman and Johnson (1964) modified by Sakai et al. (1969), which utilizes starch gel electrophoresis in a discontinuous system of buffers according to Poulik (1957). The XDH locus was analysed according to the technique of Yen and Glassman (1965) with minor modifications. The technique of Wright (1963) with modifications by Richmond (1972) was followed in the analysis of the EST-6 locus. The analysis of the i-APH locus was carried out with the technique of Beckman and