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**Original article**

# A comparison of the level of enzyme polymorphism in cosmopolitan *Drosophila* species between populations collected in distilleries and in their surroundings in Hungary

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**Summary** — The level of enzyme polymorphism was studied in populations of *Drosophila melanogaster* and *D. hydei* from three different regions of Hungary. Collections were made in distilleries or by outside baits. Allozyme variability was investigated for five loci (*Adh; Odh; Mdh; α–Gpdh; α–Amy*) by means of polyacrylamide gel electrophoresis. Two different rare alleles were detected for the *Adh* locus in *D. hydei* in Hungary. The number of species was lower in distilleries than outside. The heterozygosity level in samples from distilleries was generally lower than in samples from outside. This result gives support to the hypothesis that the more diverse the environment the higher the level of polymorphism maintained.

**enzyme polymorphism – distillery – *Drosophila hydei***

**Résumé — Comparaison du polymorphisme enzymatique chez des espèces cosmopolites de drosophiles, entre des populations Hongroises échantillonnées dans des distilleries et dans les environs.** *Le polymorphisme enzymatique a été étudié dans des populations de* Drosophila melanogaster *et de* D. hydei *issues de trois régions de Hongrie. Les récoltes ont été réalisées dans des distilleries et à l'extérieur par piégeage. La variabilité des allozymes a été étudiée en cinq locus (*Adh*; Odh; Mdh; α-Gpdh; α-Amy) par électrophorèse sur gel de polyacrilamide. Deux allèles rares ont été détectées au locus* Adh *dans les populations hongroises de* D. hydei. *Le nombre d'espèces est plus petit dans les distilleries qu'à l'extérieur. Le niveau d'hétérozygotie est en général plus bas dans les échantillons prélevés dans les distilleries qu'à l'extérieur. Ce résultat renforce l'hypothèse que le polymorphisme est maintenu à un niveau d'autant plus élevé que le milieu est plus variable.*

***polymorphisme enzymatique – distillerie* – Drosophila melanogaster – Drosophila hydei**

## Introduction

Genetic differentiation within a species is a common response to environmental heterogeneity. Some of the existing field studies indicate association between the level of polymorphism at several enzyme loci and the geographical variation of different environmen-

tal factors (Nevo, 1978; Triantaphyllidis *et al.*, 1980; Oakeshott *et al.*, 1982; Singh *et al.*, 1982; Van Delden, 1982; Oakeshott *et al.*, 1983; Nevo *et al.*, 1984).

Many authors have studied microdifferentiation of *Drosophila* populations living in wine cellars and in the surroundings (McKenzie and Parsons, 1974; Briscoe *et al.*, 1975; McKenzie and McKenzie, 1978; Parsons, 1980; McKenzie and McKenzie, 1983). Their main interest was the gene frequency distribution at the *Adh* locus in populations from the 2 types of micro-habitats. It would also be interesting, however, to study the difference in the genetic diversity of the 2 kinds of populations. In the case of laboratory populations, several observations have revealed differences in the average frequency of heterozygotes when Drosophilids were kept in homogeneous and heterogeneous environments (Powell, 1971; McDonald and Ayala, 1974; Hale and Birley, 1983).

This study provides data for a comparison of the level of polymorphism at 4 enzyme loci among village populations of *Drosophila melanogaster* and *D. hydei*, and those living in distilleries. We have found that the average frequency of heterozygotes is higher in the village populations at the investigated loci.

## Materials and Methods

Drosophilids were collected in 3 large regions of Hungary: the Central Tisza region (region I), the Bereg plain (region II) and the Sajo and Hernad valley (region III). Signs on the map (Fig. 1) show the distilleries where collection took place. Enzyme polymorphism

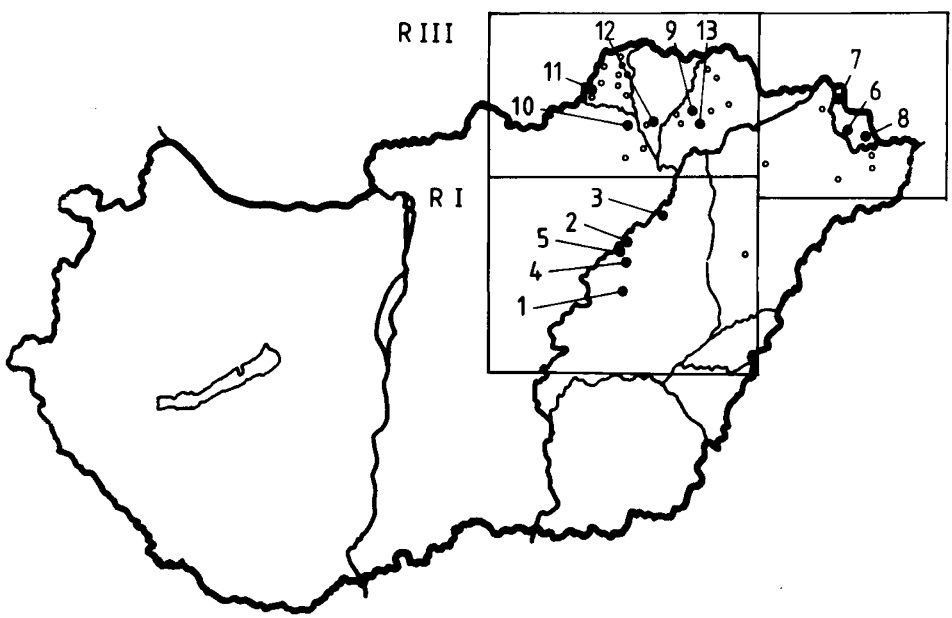


**Fig. 1.** Map showing the collection sites in the northern and eastern parts of Hungary. R I: Kunhegyes (1), Tissafured (2), Tiszacsegezs (3), Tiszaszentimre (4), Tiszaszolos (5); R II: Jand (6), Lonya (7), Tarpa (8); R III: Abaujszanto (9), Sajoszentpeter (10), Serenyfalva (11), Szikszo (12), Tallya (13). Open circles: collection in distilleries; full circles: collection both in distilleries and on baits.

was determined from 13 samples with high individual counts of both *D. melanogaster* and *D. hydei* (full circles). In order to obtain field populations we used normal maize-sucrose media as baits in the farmyards of the villages close to these distilleries. Similarly to the fermenting mash in the distilleries, this bait attracted the flies so we were able to collect them easily in the surroundings. A glass suction tube was used for the collection in both micro-habitats.

Four or 5 loci – alcohol dehydrogenase (*Adh*), octanol dehydrogenase (*Odh*), malate dehydrogenase (*Mdh*), α–glycerophosphate dehydrogenase (*α–Gpdh*) and α–amylase (*α–Amy*) – were examined in each sample. Electrophoresis was conducted on vertical polyacrylamide slabs using a discontinuous buffer system (O'Brien, 1973; Doane *et al.*, 1975; Clark, 1983; Winberg *et al.*, 1983; Batterham *et al.*, 1984). Genotype and allele frequencies were then calculated.

*Statistical procedures*

Standard errors of heterozygosity were calculated on a Commodore 64 computer by means of the Number Cruncher 1 programme.

As the proportion of heterozygotes was close to zero for most of the investigated loci, we used the angular transformation of frequency data when the *t*-tests were calculated. A paired *t*-test was performed on a Commodore 64 computer using the Number Cruncher 1 programme.

## Results

The common species in distilleries were *D. melanogaster* and *D. hydei*. Some individuals of other species also appeared, such as *D. immigrans, D. funebris* and *D. busckii*. The bait in the villages, however, attracted more species: besides the 2 common ones, we collected quite large samples of *D. immigrans* in each location and some samples of *D. funebris* and *D. busckii* in region I. Other species such as *D. repleta., D. obscura* and *D. subobscura* were scarce (Table I).

**Table I.** *Drosophila* species distribution in the 2 micro-habitats.

| *Species* | *Distillery* | *Villages* |
|---|---|---|
| *D. melanogaster* | 2 | 2 |
| *D. hydei* | 2 | 2 |
| *D. immigrans* | 1 | 2 |
| *D. funebris* | 1 | 2 |
| *D. busckii* | 1 | 2 |
| *D. repleta* | 0 | 1 |
| *D. obscura* | 0 | 1 |
| *D. suboscura* | 0 | 1 |

2 = species with large population size; 1 = scarce species; 0 = species not found

**Tableau IIa.** Allele frequencies at 5 investigated loci in *D. melanogaster* populations collected in distilleries.

| *Regions* | *RI* | | | | | *RII* | | | *RIII* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Populations* | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* |
| *Adh* sample size | 84 | 84 | 81 | 87 | 82 | 82 | 83 | 84 | 84 | 84 | 84 | 83 | 83 |
| Alleles | | | | | | | | | | | | | |
| S | 0.030 | 0.030 | 0.010 | 0.020 | 0.035 | | 0.010 | 0.010 | | 0.020 | 0.005 | 0.010 | |
| F | 0.970 | 0.970 | 0.990 | 0.980 | 0.965 | 1.000 | 0.990 | 0.990 | 1.000 | 0.980 | 0.995 | 0.990 | 1.000 |
| $\chi^2$ | 0.087 | 0.001 | 0 | 0 | 0.003 | | 0 | 0 | | 0 | 0.001 | 0 | |
| *Odh* sample size | 84 | 84 | 81 | 87 | 82 | 82 | 83 | 84 | 84 | 82 | 84 | 83 | 83 |
| Alleles | | | | | | | | | | | | | |
| S | 0.010 | 0.005 | | 0.005 | | | | | | 0.010 | | | |
| F | 0.990 | 0.995 | 1.000 | 0.995 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.990 | 1.000 | 1.000 | 1.000 |
| $\chi^2$ | 0 | 0.001 | | 0.001 | | | | | | 0 | | | |
| *Mdh* sample size | 84 | 84 | 76 | 84 | 82 | 75 | | | 84 | 56 | 70 | 82 | 84 |
| Alleles | | | | | | | | | | | | | |
| A | 0.970 | 0.980 | 0.980 | 1.000 | 1.000 | 0.980 | | | 0.985 | 0.980 | 0.970 | 1.000 | 0.990 |
| B | 0.030 | 0.020 | 0.020 | | | 0.020 | | | 0.015 | 0.020 | 0.030 | | 0.010 |
| $\chi^2$ | 0.019 | 0 | 0 | | | 0.087 | | | 0.032 | 0 | 0.002 | | 0 |
| *α–Gdph* sample size | 76 | 56 | 83 | 84 | 84 | | 84 | 70 | 68 | 84 | 84 | 82 | 80 |
| Alleles | | | | | | | | | | | | | |
| S | 0.290 | 0.352 | 0.238 | 0.236 | 0.393 | | 0.333 | 0.286 | 0.264 | 0.292 | 0.173 | 0.287 | 0.344 |
| F | 0.710 | 0.648 | 0.762 | 0.764 | 0.607 | | 0.667 | 0.714 | 0.736 | 0.708 | 0.827 | 0.713 | 0.656 |
| $\chi^2$ | 0.002 | 0.002 | 0.001 | 0.116 | 0.021 | | 0.004 | 0.007 | 0.044 | 0 | 0.017 | 0.005 | 0 |
| α–Amy sample size | 84 | 84 | 84 | 84 | 84 | | 84 | 84 | 112 | 84 | 84 | 54 | 84 |
| Phenotypes | | | | | | | | | | | | | |
| 1–3 | | | 0.012 | 0.012 | 0.012 | | 0.012 | 0.012 | | | | | 0.012 |
| 1–2 | | | | | 0.012 | | | 0.012 | | | | 0.012 | |
| 1–1 | 1.000 | 0.982 | 0.964 | 0.976 | 0.952 | | 0.988 | 0.964 | 0.976 | 0.952 | 1.000 | 0.976 | 0.988 |
| 1–1* | | 0.018 | 0.024 | 0.012 | 0.024 | | | 0.012 | 0.024 | 0.048 | | 0.012 | |

$\chi^2$ values indicate the deviation from the expectation on the basis of the Hardy-Weinberg equilibrium.

The distribution of allele frequencies at the investigated loci in *D. melanogaster* populations collected in distilleries and in villages using baits is shown in Table IIa and IIb, respectively. At the *Adh* locus, almost all the populations were polymorphic; however, the frequency of the slow allele was rather low. This is in good agreement with the European frequency gradient (Oakeshott *et al.*, 1982). The populations investigated were less polymorphic at the *Odh* than at the *Adh* locus. For the *Mdh* and *α-Amy* loci, we found that the frequencies of alternative alleles were also rather low. As the α-amylase enzyme is enco-

**Table IIb.** Allele frequency distribution at 5 investigated loci of *D. melanogaster* populations collected in villages.

| *Regions* | *RI* | | | | | *RII* | | | *RIII* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Populations* | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* |
| *Adh* sample size | 56 | 83 | 84 | 84 | 84 | 84 | 56 | 84 | 83 | 84 | 84 | 78 | 84 |
| Alleles | | | | | | | | | | | | | |
| S | 0.025 | 0.030 | 0.025 | 0.025 | 0.030 | | 0.005 | 0.010 | 0.025 | 0.020 | 0.010 | 0.025 | 0.010 |
| F | 0.975 | 0.970 | 0.975 | 0.975 | 0.970 | 1.000 | 0.995 | 0.990 | 0.975 | 0.980 | 0.990 | 0.975 | 0.990 |
| $\chi^2$ | 0.002 | 0.001 | 0.002 | 0.002 | 0.001 | | 0.002 | 0.001 | 0.002 | 0 | 0.001 | 0.002 | 0.001 |
| *Odh* sample size | 56 | 83 | 84 | 84 | 84 | 84 | 56 | 84 | 83 | 84 | 84 | 78 | 84 |
| Alleles | | | | | | | | | | | | | |
| S | 0.060 | 0.005 | | 0.010 | 0.030 | | 0.005 | | 0.010 | | 0.010 | | 0.010 |
| F | 0.940 | 0.995 | 1.000 | 0.990 | 0.970 | 1.000 | 0.995 | 1.000 | 0.990 | 1.000 | 0.990 | 1.000 | 0.990 |
| $\chi^2$ | 0.005 | 0.001 | | 0 | 0.001 | | 0.001 | | 0 | | 0 | | 0 |
| *Mdh* sample size | 56 | 84 | 84 | 84 | 84 | 84 | 84 | 84 | 82 | 71 | 84 | 82 | 89 |
| Alleles | | | | | | | | | | | | | |
| A | 0.980 | 0.990 | 0.980 | 0.990 | 0.990 | 0.960 | 0.970 | 0.970 | 0.960 | 0.970 | 0.970 | 0.990 | 0.960 |
| B | 0.020 | 0.010 | 0.020 | 0.010 | 0.010 | 0.040 | 0.030 | 0.030 | 0.040 | 0.030 | 0.030 | 0.010 | 0.040 |
| $\chi^2$ | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.002 | 0.002 | 0.086 | 0.084 | 0.002 | 0.001 | 0 | 0.001 |
| *α–Gdph* sample size | 83 | 82 | | 84 | 84 | 84 | 81 | 56 | 56 | | 56 | 82 | 80 |
| Alleles | | | | | | | | | | | | | |
| S | 0.241 | 0.305 | | 0.386 | 0.280 | 0.251 | 0.302 | 0.285 | 0.197 | | 0.170 | 0.247 | 0.253 |
| F | 0.759 | 0.695 | | 0.614 | 0.720 | 0.749 | 0.698 | 0.715 | 0.803 | | 0.830 | 0.753 | 0.747 |
| $\chi^2$ | 0.006 | 0.007 | | 0.036 | 0.043 | 0.020 | 0.007 | 0.001 | 0.018 | | 0.006 | 0.005 | 0 |
| *α–Amy* sample size | 82 | 56 | | 84 | 112 | 56 | 70 | 84 | 112 | 84 | | 84 | 84 |
| Phenotypes | | | | | | | | | | | | | |
| 1–3 | | | | | | | 0.048 | | 0.012 | | | | 0.024 |
| 1–2 | | | | | | | | 0.012 | | | | | |
| 1–1 | 0.952 | 0.988 | | 0.952 | 0.976 | 0.982 | 0.952 | 0.964 | 0.964 | 0.964 | | 0.964 | 0.952 |
| 1–1* | 0.048 | 0.012 | | 0.048 | 0.024 | 0.018 | | 0.024 | 0.024 | 0.036 | | 0.036 | 0.024 |

$\chi^2$ values indicate the deviation from the expectation on the basis of the Hardy-Weinberg equilibrium.

ded by a duplicated locus we did not calculate allele frequencies, thus only the phenotype frequencies are presented in the tables (Doane *et al.*, 1975; Singh *et al.*, 1982). At the *α-Gpdh* locus the average frequencies of the slow allele were 0.291 for the populations originating from distilleries and 0.265 for those collected in villages. On the basis of the results of a $\chi^2$ test we concluded that all the populations at all the investigated loci were in Hardy-Weinberg equilibrium.

*Drosophila hydei* was the other cosmopolitan species in our study. As opposed to *D. melanogaster*, this species did not occur in large masses either in distilleries or on bait.

The allele frequency values at all the investigated loci in *D. hydei* populations collected in distilleries and in villages by baits are presented in Table IIIa and IIIb, respectively. The *Adh* locus is known to be monomorphic in populations of *D. hydei* in the United States (Batterham *et al.*, 1984). In some of the collecting sites, however, we found 2 different rare alleles at this locus. Figure 2 shows the new genotypes. The F allele was the most common, and the rare alleles showed either faster or slower migration. These rare alleles appeared only in a few populations, mostly in region I. At the *Mdh* locus 3 alleles, *i.e.* 6 genotypes, appeared in Hungarian populations. Allele S* was found only in populations collected on baits, and the frequency of allele F was slightly higher in these popula-

**Table IIIa.** Distribution of allele frequencies at 4 investigated loci in *D. hydei* populations collected in distilleries.

| *Regions* | *RI* | | | | | *RII* | | | *RIII* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Populations* | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* |
| *Adh* sample size | 56 | 78 | 67 | 84 | 56 | 78 | 56 | 80 | 83 | 79 | 82 | 57 | 56 |
| Alleles | | | | | | | | | | | | | |
| S | | 0.010 | | | | | | | | | | | |
| F | 1.000 | 0.990 | 0.980 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| F* | | | 0.020 | | | | | | | | | | |
| $\chi^2$ | | 0.006 | 0.002 | | | | | | | | | | |
| *Mdh* sample size | 56 | 82 | | 168 | | 83 | 82 | 84 | 56 | 84 | 121 | | |
| Alleles | | | | | | | | | | | | | |
| S* | | | | | | | | | | | | | |
| S | 0.720 | 0.950 | | 0.990 | | 0.990 | 0.950 | 0.880 | 0.840 | 0.980 | 0.980 | | |
| F | 0.280 | 0.050 | | 0.010 | | 0.010 | 0.050 | 0.120 | 0.160 | 0.020 | 0.020 | | |
| $\chi^2$ | 0.044 | 0.004 | | 0.018 | | 0 | 0.005 | 0.001 | 0.001 | 0.001 | 0.001 | | |
| α–*Gdph* sample size | 84 | 75 | | | 56 | | 70 | 84 | 84 | 84 | 84 | 70 | 84 |
| Alleles | | | | | | | | | | | | | |
| S | 1.000 | 1.000 | | | 1.000 | | 0.994 | 0.994 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| F | | | | | | | 0.006 | 0.006 | | | | | |
| $\chi^2$ | | | | | | | 0 | 0 | | | | | |
| α–*Amy* sample size | 74 | 84 | | | 56 | | 56 | 84 | 84 | 84 | 83 | 84 | 84 |
| Alleles | | | | | | | | | | | | | |
| 8* | | | | | | | | | | | | 0.006 | |
| 8 | | | | | | | | 0.018 | 0.006 | 0.006 | 0.018 | 0.012 | |
| 7 | 1.000 | 1.000 | | | 1.00 | | 1.000 | 0.982 | 0.994 | 0.982 | 0.994 | 0.982 | 1.000 |
| $\chi^2$ | | | 0 | | 0 | 0 | 0 | 0 | | | | | |

$\chi^2$ values indicate the deviation from the expectation on the basis of the Hardy-Weinberg equilibrium.

**Table IIIb.** Allele frequency values at 4 investigated loci of *D hydei* populations collected in villages.

| *Regions* | *RI* | | | | | *RII* | | | *RIII* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Populations* | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* |
| *Adh* sample size | 82 | 58 | 82 | 84 | 62 | 83 | 84 | 80 | 84 | 82 | | | 83 |
| Alleles | | | | | | | | | | | | | |
| S | | 0.040 | | | 0.020 | | | | | | | | |
| F | 1.000 | 0.890 | 0.990 | 1.000 | 0.980 | 0.990 | 1.000 | 1.000 | 1.000 | 1.000 | | | 1.000 |
| F* | | 0.070 | 0.010 | | | 0.010 | | | | | | | |
| $\chi^2$ | | 0.032 | 0.005 | | 0.007 | 0.005 | | | | | | | |
| *Mdh* sample size | 84 | 65 | 84 | 84 | 68 | 83 | 83 | 84 | 66 | 56 | | | 69 |
| Alleles | | | | | | | | | | | | | |
| S* | | 0.040 | 0.010 | 0.010 | | | 0.010 | 0.010 | 0.030 | 0.010 | | | 0.050 |
| S | 0.890 | 0.890 | 0.950 | 0.930 | 0.860 | 0.960 | 0.960 | 0.960 | 0.810 | 0.920 | | | 0.810 |
| F | 0.110 | 0.070 | 0.040 | 0.060 | 0.140 | 0.040 | 0.030 | 0.030 | 0.160 | 0.070 | | | 0.140 |
| $\chi^2$ | 0.016 | 0.219 | 0.053 | 0.005 | 0.005 | 0.005 | 0.006 | 0.031 | 0.019 | 0.016 | | | 0.033 |
| α–*Gdph* sample size | 79 | 84 | 84 | | 84 | 84 | 80 | 84 | 56 | 84 | 51 | | 84 |
| Alleles | | | | | | | | | | | | | |
| S | 1.000 | 0.994 | 1.000 | | 1.000 | 0.988 | 0.988 | 0.923 | 0.957 | 1.000 | 1.000 | | 0.988 |
| F | | 0.006 | | | | 0.012 | 0.012 | 0.077 | 0.043 | | | | 0.012 |
| $\chi^2$ | | 0 | | | | 0 | 0 | 0.007 | 0.004 | | | | 0 |
| α–*Amy* sample size | 80 | 84 | 84 | 56 | 84 | 82 | 83 | 84 | 79 | 84 | 55 | | 84 |
| Alleles | | | | | | | | | | | | | |
| 8* | | | | | | | 0.006 | | | 0.006 | | | |
| 8 | 0.030 | 0.045 | | | | 0.018 | | | 0.065 | 0.006 | 0.006 | | 0.030 |
| 7 | 0.970 | 0.955 | 1.000 | 1.000 | 1.000 | 0.982 | 0.994 | 1.000 | 0.935 | 0.988 | 0.994 | | 0.970 |
| $\chi^2$ | 0 | 0 | | | | 0 | 0 | | 0 | 0 | 0 | | 0 |

$\chi^2$ values indicate the deviation from the expectation on the basis of the Hardy-Weinberg equilibrium.

tions. The *α–Gpdh* locus was actually monomorphic with rare alleles appearing mainly in region II. Similarly to the *Adh*, the *α–Amy* locus had 2 rare alleles (Doane *et al.*, 1975) that were mainly found in populations of region III.

## Discussion

We compared the level of polymorphism in populations originating from distilleries to those collected in villages in the case of both species. Some important data – as a basis of comparison – are presented in Table IV for *D. melanogaster* populations. All 3 of the parameters – proportion of polymorphic populations (frequency of rare alleles > 0.01),

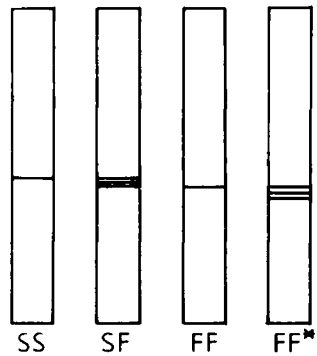


**Fig. 2.** New genotypes found at the *Adh* locus in *D. hydei* populations.

**Table IV.** The level of polymorphism in *D. melanogaster* populations originating from both microhabitats.

| *Localities* | *Distilleries* | | | | | *Villages* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Loci* | Adh | Odh | Mdh | α–Gpdh | α–Amy | Adh | Odh | Mdh | α–Gpdh | α–Amy |
| No. of populations | 13 | 13 | 11 | 12 | 12 | 13 | 13 | 13 | 11 | 11 |
| Proportion of polymorphic populations* | 0.69 | 0.15 | 0.73 | 1.00 | 0.38 | 0.85 | 0.46 | 1.00 | 1.00 | 0.75 |
| Average no. of alleles | 1.77 | 1.31 | 1.73 | 2.00 | 2.44 | 1.85 | 1.62 | 2.00 | 2.00 | 2.55 |
| Average frequency of heterozygotes | 0.026 | 0.005 | 0.025 | 0.428 | 0.020 | 0.037 | 0.020 | 0.045 | 0.416 | 0.037 |
| Standard error of heterozygosity | 0.022 | 0.008 | 0.021 | 0.063 | 0.015 | 0.020 | 0.033 | 0.020 | 0.082 | 0.011 |

*Rare allele frequency is > 0.01.

average number of alleles (each investigated allele taken into account) and average heterozygosity – indicate a higher level of polymorphism in the field as compared with the distillery populations at 4 of the investigated loci. In *D. melanogaster* the highly polymorphic *α–Gpdh* locus was, however, an exception.

In the case of *D. hydei* populations, Table V shows the most basic data for comparison. The 3 examined parameters show the level of polymorphism to be higher in village populations for 3 of the investigated loci. The only exception was the highly polymorphic *Mdh* locus.

As the average frequencies of heterozygotes have rather high standard errors, we tested the statistical significance of differences between populations originating from the 2 habitats, villages *versus* distilleries. Results of the *t*-test are shown in Table VI. The dif-

**Table V.** The level of polymorphism in *D. hydei* populations originating from both micro-habitats.

| *Localities* | *Distilleries* | | | | *Villages* | | | |
|---|---|---|---|---|---|---|---|---|
| *Loci* | Adh | Mdh | α–Gpdh | α–Amy | Adh | Mdh | α–Gpdh | α–Amy |
| No. of populations | 13 | 9 | 10 | 9 | 13 | 13 | 12 | 12 |
| Proportion of polymorphic populations | 0.15 | 1.00 | 0 | 0.33 | 0.23 | 1.00 | 0.45 | 0.42 |
| Average no. of alleles | 1.15 | 2.00 | 1.22 | 1.56 | 1.42 | 2.73 | 1.33 | 1.78 |
| Average frequency of heterozygotes | 0.003 | 0.167 | 0.003 | 0.011 | 0.028 | 0.158 | 0.032 | 0.043 |
| Standard error of heterozygosity | 0.009 | 0.135 | 0.005 | 0.015 | 0.077 | 0.101 | 0.054 | 0.045 |

ferences approached significance or were significant at all the investigated loci except *α–Gpdh* in *D. melanogaster* and *Mdh* in *D. hydei*; *i.e.*, genic diversity appears higher in the villages as compared with the distilleries.

It can be concluded that field populations had a higher level of enzyme polymorphism in comparison with those living in distilleries. This tendency clearly appears at those enzyme loci with a low heterozygosity level. A possible explanation for the situation is that both species develop in villages in more diverse resources, in fermenting windfalls, in rotting vegetables, in rubbish, etc. In distilleries, however, Drosophilids grow in a more uniform environment, on mash with rather high alcohol concentrations. It is interesting, however, that the highly polymorphic loci (*D. melanogaster: α–Gpdh, D. hydei: Mdh*) do not show such a difference.

Environments in nature are usually heterogeneous in time and space – the environment of the population has a grain structure. A fine grain would make polymorphism less

**Table VI.** Results of *t*-tests for the comparison of the arcsin transformation of the average heterozygosity between the 2 micro-habitats in both species.

| *Species* | | Adh | Odh | Mdh | α–Gpdh | α–Amy |
|---|---|---|---|---|---|---|
| *D. melanogaster* | *t* | 1.86 | 1.91 | 1.78 | 1.07 | 1.88 |
| | *P* | 0.09 | 0.08 | 0.10 | 0.32 | 0.07 |
| *D. hydei* | *t* | 3.73 | – | 0.63 | 2.31 | 1.89 |
| | *P* | 0.02 | – | 0.50 | 0.06 | 0.09 |

*t*: *t*-values; *P*: level of significance.

likely to be achieved, or would reduce the stability of polymorphism already attained (Levins and Macartur, 1966). With coarseness of grain, however, the population may maintain some choice of genotypes over the types of conditions available (Levins and Macartur, 1966; Gillespie and Langley, 1974; Taylor, 1975). Our results support the hypothesis that the more diverse the environment, the higher the level of polymorphism that can be maintained (Powell, 1971; McDonald and Ayala, 1974; Nevo *et al.*, 1984).

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