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.

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.](image-url)
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 (*Mdhh*), 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 1).

**Table 1. 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. subobscura* | 0          | 1        |

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

| Regions | RI |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
|---------|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|         |    | 1   | 2   | 3   | 4   | 5   | 6   | 7   | 8   | 9   | 10  | 11  | 12  | 13  |    |    |    |    |    |    |    |
| Populations |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |    |    |    |    |    |    |
| Adh sample size |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |    |    |    |    |    |    |
| 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 |    |    |    |    |    |    |    |
|         | χ² | 0.087 | 0.001 | 0     | 0     | 0.003 | 0     | 0     | 0     | 0.001 | 0     |     |     |     |    |    |    |    |    |    |    |    |
| Odh sample size |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |    |    |    |    |    |    |
| 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 |    |    |    |    |    |    |    |    |
|         | χ² | 0     | 0.001 | 0     | 0.001 |     | 0     |     | 0     |     | 0     | 0     | 0     |     |     |    |    |    |    |    |    |    |    |
| Mdh sample size |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |    |    |    |    |    |    |
| Alleles | A  | 0.970 | 0.980 | 0.980 | 1.000 | 1.000 | 0.980 | 0.980 | 0.970 | 1.000 | 0.990 |       |       |       |    |    |    |    |    |    |    |    |
|         | B  | 0.030 | 0.020 | 0.020 |       |       | 0.020 | 0.020 | 0.015 | 0.020 | 0.030 | 0.010 |       |       |    |    |    |    |    |    |    |    |
|         | χ² | 0.019 | 0     | 0     |       | 0.067 | 0     | 0.067 | 0     | 0.032 | 0     | 0.002 | 0     |     |    |    |    |    |    |    |    |    |
| α–Gdph sample size |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |    |    |    |    |    |    |
| 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 |     |    |    |    |    |    |    |    |    |
|         | χ² | 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 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |    |    |    |    |    |    |
| Phenotypes |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |    |    |    |    |    |    |    |
| 1–3     | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 |     |     |     |     |    |    |    |    |    |    |    |
| 1–2     | 0     | 0.012 | 0     | 0.012 | 0     | 0.012 | 0     | 0.012 | 0     | 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 | 0.012 | 0.024 | 0.012 | 0.024 | 0.048 | 0.012 |     |     |     |    |    |    |    |    |    |    |

χ² 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 Ila 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 | 84 | 56 | 84 | 83 | 84 | 84 | 78 | 84 |
| Alleles | | | | | | | | | | | | | |
| S | 0.025 | 0.030 | 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 | 0.970 | 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 | 0.001 | 0.002 | 0.001 | | |
| Odh sample size | 56 | 83 | 84 | 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 | 0.010 | | | | |
| F | 0.940 | 0.995 | 1.000 | 0.990 | 0.970 | 1.000 | 0.995 | 1.000 | 0.990 | 0.990 | 0.990 | 0.990 | 0.990 | 0.990 |
| $\chi^2$ | 0.005 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| Mdh sample size | 56 | 84 | 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 | 0.970 | 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 | 0.040 |
| $\chi^2$ | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.002 | 0.002 | 0.008 | 0.004 | 0.002 | 0.001 | 0.001 | 0.001 | 0.001 |
| $\alpha$-Gpdh sample size | 83 | 82 | 84 | 84 | 84 | 81 | 56 | 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 | 0.0 | | |
| $\alpha$-Amy sample size | 82 | 56 | 84 | 112 | 56 | 70 | 84 | 112 | 84 | 84 | 84 | | |
| Phenotypes | | | | | | | | | | | | | |
| 1-3 | 0.048 | | | | | | | | 0.024 | | | |
| 1-2 | | | | | | | | | | | | | |
| 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 $\alpha$-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 |
| F*               | 0.020 |
| χ²               | 0.006 |

| Mdh sample size | 56 | 82 | 168 | 83 | 82 | 84 | 56 | 84 | 121 |
| Alleles         |    |    |    |    |    |    |    |    |    |
| S*              | 0.720 |
| F               | 0.280 |
| F*              | 0.044 |
| χ²              | 0.004 |

| α--Gdh sample size | 84 | 75 | 56 | 70 | 84 | 84 | 84 | 84 | 70 | 84 |
| Alleles           |    |    |    |    |    |    |    |    |    |    |
| S                | 1.000 |
| F                | 0.006 |
| χ²               | 0.006 |

| α--Amy sample size | 74 | 84 | 56 | 56 | 84 | 84 | 84 | 83 | 84 | 84 |
| Alleles           |    |    |    |    |    |    |    |    |    |    |
| S*               | 0.006 |
| 8                | 0.018 |
| 7                | 1.000 |
| χ²               | 0.012 |

χ² values indicate the deviation from the expectation on the basis of the Hardy-Weinberg equilibrium.
lations. The $\alpha$-Gpdh locus was actually monomorphic with rare alleles appearing mainly in region II. Similarly to the Adh, the $\alpha$-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),
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-
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 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 |

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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References

Batterham P., Chambers G.K., Starmer W.T. & Sullivan D.T. (1984) Origin and expression of an alcohol dehydrogenase gene duplication in the genus Drosophila. Evolution 38, 644-657
Briscoe D.A., Robertson A. & Malpica J. (1975) Dominance at Adh locus is response of adult Drosophila melanogaster to environmental alcohol. Nature 255, 148-149
Clark B.A. (1983) Cytogenetic localization by variation in electrophoretic allozyme phenotype: Drosophila Odh. Biochem. Genet. 21, 375-390
Doane W.W., Abraham I., Kolar M.M., Martenson R.E. & Deibler G.E. (1975) Purified Drosophila α-amylase isozymes: genetical, biochemical, and molecular characterization. In: Isozymes. IV. Genetics and Evolution (C.L. Markert, ed), Academic Press, New York, pp. 585-607
Gillespie J.H. & Langley C.H. (1974) A general model to account for enzyme variation in natural populations. Genetics 76, 837-848
Hale C.S. & Birley A.J. (1983) The genetical response to natural selection by varied environments. II. Observations on replicate populations in spatially varied laboratory environments. Heredity 51, 581-586
Levins R. & Macartur R. (1966) Maintenance of genetic polymorphism in a heterogeneous environment: variations on a theme by Howard Levene. Am. Nat. 100, 585-590
McDonald J.F. & Ayala F.J. (1974) Genetic response to environmental heterogeneity. Nature 250, 572-574
McKechnie S.W. & McKenzie J.A. (1983) Polymorphism of alcohol dehydrogenase (ADH) in a wineyard cellular population of Drosophila melanogaster: gene frequency association with temperature and genotypic differences in progeny production Evolution 37, 850-853
McKenzie J.A. & McKechnie S.W. (1978) Ethanol tolerance and the Adh polymorphism in a natural population of Drosophila melanogaster. Nature 272, 75-76
McKenzie J.A. & Parsons P.A. (1974) Microdifferenciation in a natural population of Drosophila melanogaster to alcohol in the environment. Genetics 77, 385-394
Nevo E. (1978) Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. 13, 121-177
Nevo E., Beiles A. & Ben-Shlomo R. (1984) The evolutionary significance of genetic diversity: ecological, demographic and life history correlates. In: Evolutionary Dynamics of Genetic Diversity. (G.S. Mani, ed.), Lecture Notes in Biomathematics 53, Springer-Verlag, Berlin, pp. 13-213
Oakeshott J.C., Gibson J.B., Anderson P.R. & Knibb W.R. (1982) Alcohol dehydrogenase and glycerol-3-phosphate dehydrogenase clines in Drosophila melanogaster on different continents. Evolution 36, 86-96
Oakeshott J.G., Gibson, J.B. & Willcocks D.A. (1983) Latitudinal variation in octanol dehydrogenase and acid phosphatase allele frequencies in Drosophila melanogaster. Theor. Appl. Genet. 65, 191-196

O'Brien S.J. (1973) Comparative analysis of malate dehydrogenase of Drosophila melanogaster. Biochem. Genet. 10, 191-205

Parsons P.A. (1980) Responses of Drosophila to environmental ethanol from ecologically optimal and extreme habitats. Experientia 36, 1070-1071

Powell J.R. (1971) Genetic polymorphism in varied environments. Science 174, 1035-1036

Singh R.S., Hickey D.A. & David J. (1982) Genetic differentiation between geographically distant populations of Drosophila melanogaster. Genetics 101, 235-256

Taylor C.E. (1975) Genetic loads in heterogeneous environments. Genetics 80, 621-635

Triantaphyllidis C.D., Panourgias J.N., Scouras Z.G. & Ioanuidis G.C. (1980) Comparison of gene-enzyme variation between Drosophila melanogaster and Drosophila simulans. Genetica 51, 227-231

Van Delden W. (1982) The alcohol dehydrogenase polymorphism in Drosophila melanogaster. Evol. Biol. 15, 187-222

Winberg J., Thatcher D.R. & McKinley-McKee J.S. (1983) Drosophila melanogaster alcohol dehydrogenase: an electrophoretic study of the AdhS, AdhF and AdhUF alloenzymes. Biochem. Genet. 21, 63-80