Genet. Res., Camb. (1978), **31**, *pp.* 97–101
Printed in Great Britain

Drosophila alcohol dehydrogenase frequencies and temperature

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(*Received* 13 *July* 1977)

SUMMARY

D. melanogaster imagoes were collected weekly throughout the summer and early fall of 1976. Their *Adh* genotypes were determined by electrophoresis. The frequency of the Adh^4 isoallele fluctuated throughout the period of study. Correlation coefficients assuming no delay, one week delay, two weeks' delay, three weeks' delay, and a four-week delay of the effect of temperature on the frequency of the Adh^4 isoallele were insignificant. It was concluded that temperature alone may not be a selective factor but may be selective in combination with other environmental factors.

Ever since its discovery in natural populations of *Drosophila* and other organisms the significance of isozymic variation has remained elusive. Several experiments have indicated that isozymic variation may have adaptive value. It has been reported that the frequency of alcohol dehydrogenase (*Adh*) isoalleles vary clinally in various regions of the world (Vigue & Johnson, 1973; Grossman, Koreneva & Ulitskaya, 1970; Pipkin, Rhodes & Williams, 1973; Pipkin *et al.* 1976; Voelker, Mukai & Johnson, 1977). Environmental parameters such as average temperature and precipitation also vary clinally. Johnson & Schaffer (1973) suggested that these factors and/or other parameters may be important selective factors. Furthermore, it has been demonstrated that the *Adh* isoallele (Adh^6) which is more prevalent in the southeastern United States is more heat stable and has a higher temperature optimum than the *Adh* isoallele (Adh^4) more common in the northeastern United States (Vigue and Johnson, 1973). Johnson & Powell (1974) have shown that if *Drosophila melanogaster* imagoes are subjected to high and low temperature stresses there is a respective decrease and increase in frequency of the Adh^4 isoallele. Taken together, these experiments indicate that temperature and/or other environmental parameters may lead to differential selectivity of the *Adh* isoalleles.

If temperature and/or other factors do lead to differential selectivity of the *Adh* isoalleles, there should be a correlation between temporal changes in certain environmental parameters and temporal fluctuations in the frequencies of certain isoalleles. Dobzhansky & Ayala (1973) have reported monthly changes in the

frequencies of certain chromosomal polymorphisms and phosphoglucomutase isoalleles in *D. pseudoobscura* and *D. persimilis*, but they did not attempt to correlate these changes with any environmental parameter. Johnson & Burrows (1976) found no significant seasonal variation in *Adh*.

In the present experiment we attempt to correlate temporal fluctuations in the frequencies of *Adh* isoalleles with environmental temperature.

1. MATERIALS AND METHODS

Drosophila melanogaster imagoes were collected weekly from a suburban location in East Hartford, Connecticut, commencing in mid-June and ending in late October 1976. Standard banana bait was used as an attractant. For each collection at least 50 single fly extracts were electrophoresed and the frequencies of the respective *Adh* isoalleles determined. Details of the electrophoresis can be found in Stone *et al.* (1968). Temperature data is from United States Weather Bureau statistics as reported in the *Hartford Courant* and *Hartford Times*. Sunday through Saturday was designated as a week.

2. RESULTS AND DISCUSSION

The mechanism of maintenance of isozyme polymorphisms in natural populations is in question. The argument is mainly between those supporting selective forces and those favouring selective neutrality. Those in support of selective forces have suggested several environmental factors as the forces. We have addressed the problem by attempting to correlate temporal variation in the frequency of the *Adh* isoalleles with temporal fluctuations in environmental temperature.

As indicated in Table 1, both average weekly temperature and the frequency of the Adh^4 isoallele fluctuated throughout the period of study. Average high and average low temperatures (not shown) paralleled average temperature. Correlation coefficients assuming no delay, one week delay, two weeks' delay, three weeks' delay, and a four-week delay in the effect of temperature on the frequency of Adh^4 are 0, $-0{\cdot}06$, $-0{\cdot}28$, $0{\cdot}36$, and $0{\cdot}19$, respectively. None are significant. Correlation coefficients were similarly computed between weekly high, weekly low, average weekly high, average weekly low temperatures and the frequency of the Adh^4 isoallele. These correlations were also found to be insignificant. Thus, the data indicate that there is no exact correlation between the frequency of the Adh^4 isoallele and environmental temperature. The data do not, however, rule out the possibility that temperature in combination with other environmental factors is important. These other factors may be difficult to isolate, and the effect of their interrelationships with temperature difficult to assess. Experiments currently in progress attempt to isolate possible selective factors. We have not yet been able to demonstrate an effect of temperature on the selection of the *Adh* isoalleles using laboratory stocks derived from natural populations.

Table 1. *Average weekly temperature and frequency of* Adh^4

Week beginning	Average weekly temperature °C	Frequency *Adh*^{4}
May 30	13·4	—
June 6	17·5	—
June 13	23·2	—
June 20	25·9	—
June 27	23·6	0·34
July 4	23·6	0·48
July 11	22·2	0·64
July 18	22·9	0·57
July 25	20·6	0·53
August 1	20·8	0·47
August 8	23·7	0·42
August 15	21·3	0·51
August 22	23·9	0·53
August 29	16·9	0·57
September 5	18·0	0·47
September 12	20·6	0·57
September 19	15·8	0·59
September 26	13·8	0·51
October 3	17·4	0·66
October 10	10·3	0·54
October 17	6·5	0·44

The current data apparently contradict that of Johnson & Powell (1974) who seem to demonstrate temperature as a selective agent for the *Adh* isoalleles. At no time during our study, however, did the air temperature reach the extremes used by Johnson and Powell (approximately 4 °C and 41 °C). Surface temperatures, however, could have reached the 41 °C extreme, but it is unlikely that the 4 °C extreme was reached. In the light of the Johnson and Powell data it is possible that our findings of no significant correlation between *Adh* frequencies and temperature results from the fact that only extreme temperatures as reported by Johnson and Powell are selective.

The data clearly show that the frequencies of the *Adh* isoalleles vary seasonally. The frequency of *Adh*^{4} varied from 0·34 to 0·66. We have collected from only one site and are, therefore, unable to make intersite comparisons. We have been collecting from the same site since June, 1977, and there is a remarkable similarity between data collected this year and that collected in 1976. Thus, the variation seems to be repeatable from year to year.

Taken over the entire collection period the frequency of *Adh*^{4} was 0·46 which falls on the cline described by Vigue & Johnson (1973). It could be argued that since there is considerable seasonal variation in the frequencies of *Adh* the cline is a result of collecting at various times of the year. Collections which gave rise to the clinal data were made throughout the year. This seems unlikely, however, since seasonal variation may not occur in all localities. Johnson & Burrows (1976) reported no significant seasonal variation in North Carolina. In addition,

the seasonal variation we report here is considerably less than the variation found on the cline. Furthermore, the Mexican cline described by Pipkin *et al.* (1973) for *Adh* was derived from data collected in a relatively short period of time (two weeks).

It could also be argued that the seasonal variation is not due to selection at the *Adh* locus but at some other locus or loci contained within a chromosomal inversion. We have not yet surveyed this population for inversions. It is thought, however, that the frequency of any inversion is low since Voelker *et al.* (1977) reported that inversions are infrequent or absent in northern populations. In any event the relative contribution of linkage disequilibrium between isoalleles and inversions in maintaining isoalleles in populations is unknown. In some populations there seems to be significant linkage disequilibrium between certain inversions such as *In* (*2L*)*t* and *Adh*. In other populations there is no disequilibrium and in still other populations inversions are absent.

It is possible that seasonal variation is due to 'rapid and extensive local migration' as reported by Johnson & Burrows (1976). At present there is little data on the migration of *Drosophila* and the contribution of migration to seasonal variation would be impossible to assess. Thus, the contribution of migration to both seasonal and geographical variation must be included in any model for the mechanism of maintenance of such variation.

Currently, the most viable hypothesis is that geographical and seasonal variation result from selection with a possible contribution of migration. Verification of the hypothesis awaits conclusive identification of selective factors and the confirmation that the factors are operable in the natural environment.

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