Sci. Annals, Fac. Phys. & Mathem., Univ. Thessaloniki, 21, 59 (1981)

LINKAGE DISEQUILIBRIUM IN GREEK POPULATIONS OF DROSOPHILA MELANOGASTER AND DROSOPHILA SIMULANS

by

C. D. TRIANTAPHYLLIDIS, Z.G. SCOURAS and A. G. KOUVATSI
(Laboratory of General Biology, University of Thessaloniki)

(Received 16.4.81)

Abstract: *Six wild Greek sympatric populations of Drosophila melanogaster and D. simulans were studied to determine whether linkage disequilibrium exists between some allozyme loci. The obtained results indicate that there is linkage equilibrium between the enzyme loci studied in D. simulans, while there is linkage disequilibrium between aGpdh and Adh loci in D. melanogaster. The latter finding is briefly discussed.*

INTRODUCTION

On the basis of computer simulation experiments were suggested (Wills et al 1970) that in natural populations a large number of polymorphisms could be maintained together with a considerable mangitude of linkage disequilibrium. Furthermore, it was proposed (Franklin and Lewontin 1970) that nonrandom associations between selectively maintained linked loci might be quite frequent. Evidence of linkage disequilibrium between loci and inversions (i. e. Kojima et al 1970) and between pairs of allozyme loci in *Drosophila* (i. e. O' Brien and McIntyre 1971) was soon reported. In the past years, there have been numerous publications describing studies of linkage disequilibrium between alleles at electrophoretically detected loci in various species of *Drosophila*. These include the studies of *D. melanogaster* populations by Mukai et al (1971), Charlesworth and Charlesworth (1973), Mukai et al (1974), Langley et al (1974), Mukai and Voelker (1977), Langley et al (1977) and Langley et al (1978), as well as studies in other *Drosophila* species.

The general conclusion from the above studies seems to be that linkage disequilibrium between allozyme loci is not as common, with

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one or two exceptions, as suggested by the early studies.

In the present paper, we report data on linkage disequilibrium on aGpdh, Adh and Mdh loci from six wild Greek populations of *D. melanogaster*. Furthermore, since the linkage group involving several allozyme systems of *D. simulans* has been assigned (see Ohnishi and Voelker for a review, 1979) it is worthwhile to test whether linkage disequilibrium exists between third chromosome allozyme markers in this species.

MATERIALS AND METHODS

The flies used in this study were collected at Doirani (September 1979), University Farm of Thessaloniki (June and September 1979), Drosseron, Trikala (October 1979), Benitses, Corfu (September 1978), Sparti (August 1979), Petalidion, Kalamata (September 1980) and Tybakion, Creta (September 1980). Allozyme allele frequencies were estimated by horizontal starch gel electrophoresis of the wild-caught flies. The methods used were essentially those of Triantaphyllidis et al (1980). The loci assayed, their International Union of Biochemistry numbers, genetic map position and buffer systems are given in Table 1.

TABLE 1

The table shows allozymes assayed, their International Union of Biochemistry numbers, genetic map position, buffer systems and references for the genetic position

Allozyme	I.U.B. code number	Map position	B*	References
D. melanogaster				
α-glycerophosphate dehydrogenase (aGpdh)	(1.1.1.8)	2-17.8	I	Grell 1967
malate dehydrogenase (Mdh)	(1.1.1.37)	2-35.3	I	O'Brien 1969
alcohol dehydrogenase (Adh)	(1.1.1.1)	2-50.1	I	Grell et al 1965
D. simulans				
esterase-6 (Est-6)	(3.1.1.2)	3-25.2	II	Wright and McIntyre 1963
phosphoglucomutase (Pgm)	(2.7.5.1)	3-38.1	I	Ohnishi and Voelker 1979
acid phosphatase (Acph-1)	(3.1.3.2)	3-134	I	McIntyre 1966

B*=Buffers: I- see Ayalla et al 1972
II- see Ashton et al 1961

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TABLE 2

Observed phenotypic combinations between linked allozymes in Greek *D. melanogaster* populations

Allozyme loci	Location	Year	Phenotypic combinations									N	χ^2	DF*	P
			S/S	S/SF	S/F	SF/S	SF/SF	SF/F	F/S	F/SF	F/F				
aGpdh-Mdh	Total		168	3	1	519	10	0	676	14	2	1393	0.28	2	>0.70
aGpdh-Adh	Doirani	1979	0	0	6	1	8	70	1	40	108	234	9.23	1	<0.01
	Un. Farm	1979a	3	1	18	3	13	75	7	40	100	260	10.63	4	<0.05
	Un. Farm	1979b	0	0	15	1	13	46	6	45	87	213	7.66	1	<0.01
	Drosseron	1979	1	1	19	0	14	68	7	35	85	230	9.27	1	<0.01
	Corfu	1978	0	0	20	0	3	78	4	6	45	156	8.88	1	<0.01
	Petalidion	1980	1	1	54	0	11	115	6	22	71	281	23.00	1	<0.001
	Tybakion	1980	1	6	49	2	19	76	3	13	25	194	8.82	4	0.1>P>0.05
	Total		6	9	181	7	81	528	34	201	521	1568	87.00	4	<0.01

*=Degrees of freedom, a=June 1979, b=September 1979.

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TABLE 3

Observed phenotypic combinations between linked allozymes in Greek *D. simulans* populations

Allozyme loci	Location	Year	Phenotypic combinations									N	χ^2	DF*	P
			S/S	S/SF	S/F	SF/S	SF/SF	SF/F	F/S	F/SF	F/F				
Est-6-Acph	Doirani	1979	0	8	6	1	26	43	8	60	90	242	1.69	2	>0.10
	Un. Farm	1979[b]	2	6	14	4	35	45	10	58	85	259	1.40	4	>0.70
	Drosseron	1979	3	8	11	6	36	40	15	63	58	240	1.70	4	>0.70
	Corfu	1978	2	3	3	2	11	15	0	10	15	61	0.99	2	>0.50
	Sparti	1979	1	8	14	7	23	42	12	43	90	240	0.56	4	>0.95
	Petalidion	1980	0	6	15	2	33	50	9	50	69	234	2.38	2	>0.10
	Total		8	39	63	22	164	235	54	284	407	1276	2.20	4	>0.70
Pgm-Acph	Drosseron	1979	1	3	1	2	23	32	12	67	86	227	1.40	4	>0.70
	Petalidion	1980	0	0	3	0	9	17	5	26	67	127	0.004	1	>0.70
	Total[x]		1	3	4	3	35	51	17	96	170	380	1.20	4	>0.70

x=Twenty six individuals were added from Tybakion.

*, b=Same as Table 2.

RESULTS

Tables 2 and 3 contain the observed numbers of phenotypic combinations for various two-locus comparisons of linked allozyme loci of *D. melanogaster* and *D. simulans* respectively. Joint genotypic frequency distributions for pairs of polymorphic loci were examined for possible linkage disequilibria by means of the x^2 contingency method (Socal and Rohlf 1969). The hypothesis of independence (i. e. that phenotypes at the two loci are distributed independently) has been tested using a row-by-column test of independence. In some cases the data were pooled because of the small numbers of some of the phenotypic combinations involving the rarest alleles. The obtained x^2 results for *D. melanogaster* and *D. simulans* are given in Tables 2 and 3 respectively.

DISCUSSION

In the present investigation 6 different enzyme loci have been studied with regard to the existence of nonrandom associations between some pairs of them. The data do not show significantly detectable linkage disequilibrium between Est-6 vs Acph and PGM vs Acph allozyme loci in the *D. simulans* Greek populations examined. This is also the case for aGpdh vs Mdh genes in the *D. melanogaster* Greek populations analysed. On the other hand, the Doirani, University Farm, Drosseron, Corfu and Petalidion *D. melanogaster* populations show linkage disequilibrium between aGpdh and Adh loci, while the Tybakion population approaches significance ($0.10 > P > 0.05$). Thus, the *D. melanogaster* findings are quite different from previous results reported by Mukai et al (1974), Alahiotis (1975), Mukai and Voelker (1977), Voelker et al (1977); but see also Langley et al (1978).

Two alternative hypothesis can be postulated to explain the observed linkage disequilibrium between the aGpdh and Adh loci. First, our findings of nonrandom association between the aGpdh and Adh loci of *D. melanogaster* may be well the results of intense selective forces acting on the Adh and aGpdh loci (see Voelker et al 1977 and Triantaphyllidis et al, 1982). Second, the observed linkage disequilibrium between the two allozyme loci may be the results of nonrandom association between:

a) the Adh locus and a second chromosome inversion; complete

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association between the Adh^S allele and the In (2L)t inversion has been described by several authors (i. e. Kojima et al 1970, Mukai et al 1971, Mukai et al 1974, Langley et al 1974, Mukai and Voelker 1977, Voelker et al 1977).

b) the aGpdh locus and a second chromosome inversion; a significant association between the aGpdh loci and the In (2L)t inversion has been reported by Langley et al (1974).

c) the aGpdh and Adh allozyme loci and second chromosome inversions; Alahiotis and Pelecanos (1978) state that nonrandom association exist between the allozymes of these two loci and the In (2L)t and In(2R)52A-56F inversions in a Greek natural population. Hence, the question of the origin of the linkage disequilibrium between the aGpdh and the Adh loci in the studied populations remains open. The answer will be found when the same wild *D. melanogaster* populations would be studied for allozyme and inversion polymorphisms simultaneously.

In summury, we may conclude that our data do not show singificantly detectable linkage disequilibrium between the allozyme loci studied in the Greek populations examined. Thus, our results are consistent with the concept that linkage disequilibrium between linked allozyme loci is the exception rather than the rule.

Acknowledgement. C. T. gratefully acknowledges the financial assistance of the Greek National Research Center for a part of this research. We thank Mrs Eutyhia Karamitrou-Kouskounelou for her help.

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ΠΕΡΙΛΗΨΗ

ΑΝΙΣΟΡΡΟΠΙΑ ΣΥΝΔΕΣΗΣ ΣΕ ΕΛΛΗΝΙΚΟΥΣ ΠΛΗΘΥΣΜΟΥΣ DROSOPHILA MELANOGASTER ΚΑΙ DROSOPHILA SIMULANS

ὑπὸ

Κ. Δ. ΤΡΙΑΝΤΑΦΥΛΛΙΔΗ - Ζ. Γ. ΣΚΟΥΡΑ - Α. Γ. ΚΟΥΒΑΤΣΗ

('Εργαστήριο Γενικῆς Βιολογίας Πανεπιστημίου Θεσσαλονίκης)

Στὴν ἐργασία μελετήσαμε 6 Ἑλληνικοὺς συμπατρικοὺς πληθυσμοὺς *Drosophila melanogaster* καὶ *Drosophila simulans* προκειμένου νὰ ἐλέγξουμε ἂν ὑπάρχει ἀνισορροπία σύνδεσης ἀνάμεσα σὲ μερικὰ συνδεμένα γονίδια ποὺ καθορίζουν ἀλλοένζυμα. Τὰ ἀποτελέσματά μας ἔδειξαν ὅτι τὰ γονίδια Est-6 - Acph καθὼς καὶ τὰ γονίδια PGM - Acph τῆς *D. simulans* - στὰ ὁποῖα ἀπὸ ὅτι γνωρίζουμε γίνεται μελέτη ἀνισορροπίας σύνδεσης γιὰ πρώτη φορὰ—βρίσκονται σὲ ἰσορροπία σύνδεσης. Ἀντίθετα, τὰ γονίδια αGpch καὶ Adh τοῦ εἴδους *D. melanogaster* βρίσκονται σὲ ἀνισορροπία σύνδεσης. Προτείνουμε διάφορες ὑποθέσεις γιὰ νὰ ἐξηγήσουμε τὸ ἀποτέλεσμα αὐτό.

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