Heredity **54** (1985) 209–217

Received 3 September 1984

Enzymatic and quantitative variation in European and African populations of *Drosophila simulans*

P. Hyytia,
P. Capy,
J. R. David and
***R. S. Singh**

Laboratoire de Biologie et Génétique Evolutives CNRS, 91 190 Gif sur Yvette, France;
*** Department of Biology, McMaster University, Hamilton, Ontario Canada L8S 4K1.**

Allozyme polymorphism at 15 loci of *D. simulans* was studied in 7 natural populations from Europe, North and tropical Africa. Morphological traits were studied in nine European and eleven Afrotropical strains.

Within a population, the biochemical polymorphisms of *Drosophila simulans* and its sibling *Drosophila melanogaster* are not very different, although *D. simulans* has a lower heterozygosity. Between-populations genetic differentiation is however much lower in *D. simulans* than in *D. melanogaster*. Several loci of *D. simulans* do exhibit latitudinal trends but these are relatively weak.

For morphological traits, both species show an increase of size with latitude, but geographic variation is again less pronounced in *D. simulans*. Both species are native to tropical Africa and have colonised the rest of the world. During this process, *D. simulans* has undergone much less geographic differentiation than has *D. melanogaster*, so that the ecological success of the two species is not correlated with similarities in their genetic properties.

INTRODUCTION

Among about 2500 species known in the drosophilid family (Wheeler, 1981), only 21 have a subcosmopolitan status, in that they exist in at least three non-adjacent biogeographic realms (David and Tsacas, 1981). All these species occupy their present geographic range as a result of involuntary transport by man. Among the 21 species, the sibling *D. melanogaster* and *D. simulans* are especially interesting since they are the only two which possess large populations in both tropical and temperate conditions (David and Tsacas, 1981). Many studies of the ecology, ecophysiology and genetics of these domestic species have attempted to understand their population dynamics, ecology and other reasons of which may underlie their demographic success (*e.g.*, Parsons, 1975; 1980*a*; 1983; Parsons and Stanley, 1981).

Populations of *D. melanogaster*, are genetically highly differentiated, for chromosomal polymorphism (Ashburner and Lemeunier, 1976; Watanabe and Watanabe, 1977; Voelker *et al.*, 1978; Stalker, 1980; Knibb *et al.*, 1981), allozyme variation (Kojima *et al.*, 1970; Band, 1975; Mettler *et al.*, 1977; Triantaphyllidis *et al.*, 1980; 1982; Oakeshott *et al.*, 1981*a*, *b*; David, 1982; Singh *et al.*, 1982; Capy *et al.*, 1983; Anderson and Oakeshott, 1984),.biometrical traits (Teissier, 1956; Tantawy and Mallah, 1960; David *et al.*, 1976; 1977; Capy *et al.*, 1983) and physiological traits (David and Bocquet, 1975; Allemand and David, 1976; David *et al.*, 1977; Cohet *et al.*, 1980; Parsons, 1980*b*, *c*; Bouletreau-Merle *et al.*, 1982). Several authors argue that this extensive genetic differentiation is one cause of the demographic success of *D. melanogaster* under a variety of ecological conditions.

D. simulans is closely related to *D. melanogaster* and shows comparable ecological success. We might hence expect a comparable genetic differentiation among its populations. However, although *D. simulans* is far less studied it already appears that, for a variety of traits, it is less variable than *D. melanogaster*. For example, natural populations are monomorphic for their chromosome structures (Ashburner and

Lemeunier, 1976); the species does not exhibit a latitudinal cline for ethanol tolerance (David and Bocquet, 1975); its protein polymorphism, studied with 2-dimensional electrophoresis, is lower than in *D. melanogaster* (Onishi *et al.*, 1982). Surprisingly few studies have been devoted to allozyme polymorphism in *D. simulans* (O'Brien and MacIntyre, 1969; Berger, 1970; Triantaphyllidis, 1973; Steiner *et al.*, 1976; Triantaphyllidis *et al.*, 1980; Salam *et al.*, 1981; 1982; Cabrera *et al.*, 1982; Onishi *et al.*, 1982; Anderson and Oakeshott, 1984) and most of these concern temperate populations.

D. melanogaster and *D. simulans* are now known to be native to tropical Africa (Tsacas and Lachaise, 1974; David and Tsacas, 1981) and in *D. melanogaster*, there is extensive genetic divergence between the ancestral, Afrotropical populations and the European ones. Here we compare the allozyme polymorphism of seven natural populations of *D. simulans* from Europe, North and tropical Africa (mainland and islands). Differences in metric characters are often easier to detect than are differences in gene frequencies (*e.g.*, Lewontin, 1984) and are generally thought to be more directly subject to natural selection than are allozymes (Kimura, 1983). Our analysis has hence been extended to include morphological comparisons between French and Afrotropical populations of *D. simulans* and *D. melanogaster*.

MATERIALS AND METHODS

Wild living females were used to initiate isofemale lines. Two adult flies were electrophoresed from each line after a few generations (from 1 to 10) of laboratory culture. The populations sampled were from Villeurbanne, France (20 lines), Antibes, France (23 lines), Athens, Greece (25 lines), Nasrallah, Tunisia (42 lines), Brazzaville, Congo (39 lines), Mahé, Seychelles islands (23 lines) and Tananarive, Madagascar (26 lines).

Methods of starch gel electrophoresis were adapted from Shaw and Prasad (1970) and Ayala *et al.*, (1972), and 15 different gene-enzyme loci were studied in each population. Alleles were characterised by their migration distance on the gel, the most common one receiving the arbitrary value of 1·00. Expected heterozygosity was calculated (assuming Hardy–Weinberg equilibrium) for each locus and populations. Few enzyme loci are mapped in *D. simulans*. However, in all cases, an homology could be established with an already identified locus of *D. melanogaster* and we have used the same nomenclature for describing enzyme systems in each species. Moreover, we have also indicated when alleles with identical mobilities were observed in the two species.

Biometrical analysis was performed on 9 French and 11 Afrotropical strains. Each strain was founded by several (in most cases more than 10) females and kept in the laboratory as a mass culture in bottles. Larvae were grown at 25°C at low density on a killed yeast medium and for each strain, six different traits were measured on 30 different adults. These traits were fresh adult weight (taken a few hours after emergence), wing and thorax lengths, sternopleural and abdominal chaetae numbers and ovariole number in females (see David, 1979 for more details). Viability and duration of development were also measured for each strain, starting from a sample of 300 eggs (see David *et al.*, 1976, for techniques).

RESULTS

Allozyme frequencies

Five of the 15 loci studied: ADH (alcohol dehydrogenase), FU (fumarase), HK-3 (hexokinase 3), ME (malic enzyme) and 6-PGD (6 phosphogluconate dehydrogenase) were monomorphic in all populations.

The most polymorphic loci (table 1) as shown by average expected heterozygosities (table 2) are EST-C (esterase-C), EST-6 (esterase 6), ACPH (acid phosphatase), PGM (phospho-glucomutase), XDH (xanthine dehydrogenase), ALDOX (aldehyde oxidase) and HK-1 (hexokinase 1). These results generally confirm what was already found by previous authors with the exception of HK-1 (Kojima *et al.*, 1970; Onishi *et al.*, 1982 and Cabrera *et al.*, 1982) which was previously found to be polymorphic (2 alleles) only at low heterozygosity (0·019) in a single Spanish population. ADH is generally monomorphic in *D. simulans* and we failed to find any rare alleles, although such alleles have been reported from other parts of the world: such as Texas (Kojima *et al.*, 1970); Hawaii (Steiner *et al.*, 1976) and Spain (Cabrera *et al* 1982). α-GPDH is monomorphic in most *Drosophila* species (Lakovaara and Keranen, 1980), although rare alleles in *D. simulans*, are known from Texas (Kojima *et al.*, 1970), Hawaii (Steiner *et al.*, 1976) and Greece (Triantaphyllidis *et al.*, 1980).

Table 3 shows that, in most populations, about half of the 15 loci sampled were polymorphic with a mean of 2 alleles per locus and an average heterozygosity of 16 per cent. Differences between populations are generally small, although more

Table 1 Frequency of alleles in populations of *Drosophila simulans*. Alleles marked * exhibit the same mobility as alleles found in *D. melanogaster*

Locus and Allele	France Villeurb. 45·7°N	France Antib. 43·6°N	Greece 38°N	Tunisia 35°6N	Congo 4°2S	Seychelles 3·8°S	Madagascar 18·7°S	Average
ACPH: acid phosphatase								
0·95	0·300	0·200	0·250	0·131	0·087	0·130	0·039	0·150
1·00	0·700	0·800	0·729	0·851	0·873	0·870	0·913	0·829
1·06	···	···	0·021	0·018	0·040	···	0·048	0·021
Het.	0·420	0·320	0·406	0·258	0·229	0·226	0·163	0·288 ± 0·096
ALDOX: aldehyde oxidase								
1·00	0·744	0·767	0·910	0·792	0·967	1·000	0·962	0·880
1·03	0·256	0·233	0·090	0·208	0·033	···	0·038	0·120
Het.	0·381	0·357	0·164	0·329	0·064	0	0·073	0·195 ± 0·158
EST-C: Esterase C								
0·87	···	···	···	···	···	···	0·010	0·001
0·89	···	···	···	···	···	···	0·010	0·001
0·93	0·138	0·267	0·217	0·274	0·058	0·239	0·049	0·175
0·96	0·338	0·289	0·152	0·360	0·026	0·141	0·186	0·207
1·00	0·475	0·256	0·522	0·183	0·377	0·500	0·363	0·364
1·02	0·025	0·167	0·087	0·171	0·507	0·109	0·324	0·226
1·04	0·025	0·022	0·022	0·012	0·032	0·011	0·059	0·026
Het.	0·640	0·751	0·649	0·732	0·596	0·661	0·723	0·679 ± 0·057
EST-6 esterase 6								
0·87	···	···	···	···	0·182	0·207	···	0·060
0·93	···	0·067	···	···	0·020	···	0·020	0·014
0·96*	0·350	0·244	0·292	0·429	0·442	0·329	0·340	0·362
1·00*	0·650	0·689	0·667	0·544	0·357	0·427	0·530	0·537
1·03	···	···	0·042	0·018	···	0·037	0·090	0·024
1·04	···	···	···	···	···	···	0·020	0·003
Het.	0·455	0·462	0·468	0·509	0·644	0·665	0·595	0·542 ± 0·090
α-GPDH: α-Glycerophosphate deydrogenase								
0·95	···	···	···	···	0·013	···	···	0·003
1·00*	1·000	1·000	1·000	1·000	0·987	1·000	1·000	0·997
Het.	0	0	0	0	0·025	0	0	0·004 ± 0·009
HK-1: hexokinase 1								
0·97	···	···	0·020	···	0·036	0·100	0·173	0·045
1·00*	0·971	0·964	0·970	0·963	0·869	0·837	0·808	0·915
1·03	0·029	0·036	0·010	0·037	0·095	0·063	0·019	0·040
Het.	0·066	0·069	0·059	0·071	0·235	0·285	0·317	0·157 ± 0·116
MDH-C: malate dehydrogenase, cytoplasmic								
1·00*	1·000	1·000	1·000	1·000	1·000	1·000	0·990	0·998
1·04	···	···	···	···	···	···	0·010	0·002
Het.	0	0	0	0	0	0	0·020	0·003 ± 0·007
ODH: octanol dehydrogenase								
0·96*	0·088	0·011	0·021	···	···	···	0·020	0·015
1·00*	0·912	0·989	0·979	1·000	0·981	1·000	0·970	0·980
1·04	···	···	···	···	0·019	···	0·010	0·005
Het.	0·161	0·022	0·042	0	0·037	0	0·059	0·046 ± 0·055
PGM: phospho-gluco-mutase								
0·93	0·038	0·067	0·135	0·024	···	0·109	···	0·047
0·94	0·125	0·089	0·010	0·095	0·039	···	0·019	0·054
1·00*	0·838	0·789	0·854	0·881	0·890	0·739	0·952	0·857
1·06	···	0·055	···	···	0·071	0·152	0·029	0·042
Het.	0·281	0·362	0·252	0·214	0·201	0·419	0·092	0·260 ± 0·108
XDH: xanthine dehydrogenase								
0·98	0·044	0·214	0·210	0·106	0·143	0·175	0·067	0·135
1·00	0·956	0·786	0·790	0·894	0·857	0·825	0·933	0·865
Het.	0·084	0·336	0·332	0·190	0·245	0·289	0·125	0·228 ± 0·099

Table 2 Comparison of polymorphism within and between populations for polymorphic loci of *D. simulans*. Fixation index is HT-$\bar{H}$S/HT; for 8 highly polymorphic loci. Chi square values and numbers of degrees of freedom (in brackets) are given (all values are statistically significant, $p < 0{\cdot}01$)

Loci	Within popul. heteroz. ($\bar{H}_S$)	Total heteroz. (H_T)	Fixation index $\left(\frac{H_T - \bar{H}_S}{H_T}\right)$	Chi-square (df)
ACPH	0·288	0·302	0·043	38·9 (6)
ALDOX	0·196	0·215	0·091	68·1 (6)
EST-C	0·684	0·754	0·094	214·3 (20)
EST-6	0·542	0·569	0·048	116·4 (13)
α-GPDH	0·004	0·004	0	—
HK-1*	0·157	0·165	0·053	44·33 (3)
MDH-c	0·003	0·003	0	—
ODH	0·046	0·047	0·035	34·7 (6)
PGM	0·260	0·271	0·041	23·5 (6)
XDH	0·229	0·236	0·033	20·5 (6)
mean (10 polym. loci)	0·241	0·253	0·046	
mean (all 15 loci)	0·161	0·168	0·031	

* Chi-square test done between the 4 temperate and the 3 tropical populations.

numerous alleles were found in two of the tropical populations from Congo and Madagascar.

Previously published estimates for heterozygosity of *D. simulans* range from 0·059 (Onishi *et al.*, 1982) to 0·173 (Triantaphyllidis *et al.*, 1980). However, these variations largely reflect differences in the number of loci sampled and the choice of loci and figures for the same locus studied by different authors, do not show great differences between populations. Although the proportion of polymorphic loci in one Japanese population (Onishi *et al.*, 1982), is 0·29, all other observed values fall between 0·41 and 0·46, not very different from 0·52 obtained by ourselves. The average number of alleles per locus varies from 1·46 (Cabrera *et al.*, 1982) to 2·07 (Triantaphyllidis *et al.*, 1980), thus including the value of 2·00 found here.

How much genetic divergence is there between geographically distant populations of the cosmopolitan specie *D. simulans*? An homogeneity Chi-square test on the 8 highly polymorphic loci shows that there is a highly significant geographic heterogeneity (table 2). A more general method of comparing the total heterozygosity to within population heterozygosity is given by Wright's fixation index F_{ST} (table 2). The observed values are generally low, with an average of 0·046 for the 10 polymorphic loci. As in *D. melanogaster* (Singh *et al.*, 1982), F_{ST} is not correlated with average heterozygosity.

Although there is significant heterogeneity among populations, there are no significant correlations between allele frequencies and latitude. Table 1 does suggest that there is a weak latitudinal trend for four loci. For ACPH$^{0.95}$ and EST-6$^{1.00}$, we note a decrease of allele toward the Equator. For ALDOX, the frequency of the 1·00 allele increases in tropical populations, and the HK-1 polymorphism of the 4 temperate populations is significantly lower than is that of those in the

Table 3 Summary of allozyme polymorphism in various populations of *Drosophila simulans*

	Villeurbanne (France)	Antibes (France)	Greece	Tunisia	Congo	Seychelles	Madagascar	Average
proportion polym. loci*	0·53	0·53	0·53	0·47	0·60	0·40	0·60	0·52
alleles per locus	1·80	1·93	2·00	1·87	2·13	1·87	2·40	2·00
average heterozygosity: 10 polymorphic loci	0·249	0·269	0·237	0·230	0·228	0·255	0·217	0·241
average heterozygosity: all 15 loci	0·166	0·179	0·158	0·254	0·152	0·170	0·145	0·161

* Calculated at 1 per cent level.

Table 4 Genetic identities (above diagonal) and genetic distances (below diagonal) between geographical populations of *D. simulans*

Populations	Anti.	Vill.	Gree.	Tuni.	Congo	Seych.	Madag.
Antibes		0·992	0·992	0·991	0·971	0·944	0·982
Villeurbanne	0·008		0·993	0·996	0·977	0·948	0·985
Greece	0·008	0·007		0·988	0·980	0·955	0·987
Tunisia	0·009	0·004	0·012		0·981	0·947	0·988
Congo	0·029	0·023	0·019	0·019		0·954	0·992
Seychelles	0·057	0·054	0·046	0·054	0·048		0·963
Madagascar	0·018	0·016	0·013	0·012	0·008	0·037	

tropics. Finally, for PGM, an increase of heterozygosity with latitude is observed, if we exclude the very isolated Seychellian population. Similar latitudinal tendencies have already been noticed for 3 of these loci (EST-6, ACPH and PGM) in Greece over a much shorter geographic range by Triantaphyllidis *et al.*, (1982) who did not study HK-1 and ALDOX. In a survey of numerous populations from several continents, Anderson and Oakeshott (1984) found a latitudinal cline for EST-6 but did not find any significant variation for PGM. The problem of geographical trends in *D. simulans* loci will become clear only with the study of more populations for various parts of the world.

Genetic identities and genetic distances between populations were calculated according to Nei (1972) and are given in table 4. The distances ranged from 0·008 to 0·057 with an average of 0·024 ($n = 21$). Distances between the 4 temperate and the 3 tropical populations are significantly ($p < 0·05$) higher ($D = 0·030 + 0·005$; $n = 12$) than between populations living under similar climatic conditions ($D = 0·016 + 0·005$; $n = 9$). Tropical populations are more diverse and heterogeneous than the temperate ones. This could reflect their greater geographic distances. The Seychellian population, which is an isolated and small population with special ecological needs (David and Tsacas, unpublished) is the most different from all others (see also fig. 2).

Quantitative data

The results obtained for 9 French and 11 tropical African populations are given in table 5. For all biometrical traits (from fresh weight to ovariole number) the average values are lower in African

Table 5 Comparison of French and Afrotropical strains in *Drosophila simulans* and *Drosophila melanogaster* for various quantitative traits. Statistical significance: *($p < 0·05$), **($p < 0·01$)

		D. simulans			*D. melanogaster*		
Traits	Sex	France ($n = 9$)	Trop. Africa ($n = 11$)	Difference	France ($n = 30$)	Trop. Africa ($n = 22$)	Difference
Fresh weight (mg-10^{-2})	♀	109·24 ± 2·17	93·97 ± 1·16	15·27 ± 2·33**	123·22 ± 0·81	103·37 ± 1·01	19·85 ± 1·28**
	♂	87·32 ± 1·83	73·63 ± 1·67	13·69 ± 9·47**	91·91 ± 0·73	78·03 ± 0·94	13·88 ± 1·17**
Thorax length (mm-10^{-2})	♀	105·72 ± 0·46	102·04 ± 0·62	3·68 ± 0·80**	107·61 ± 0·37	102·14 ± 0·58	2·14 ± 0·66**
	♂	94·29 ± 0·63	90·39 ± 0·64	3·90 ± 0·90**	95·23 ± 0·39	88·74 ± 0·46	6·49 ± 0·60**
Wing length (mm-10^{-2})	♀	197·29 ± 1·64	191·23 ± 2·54	6·06 ± 3·19*	227·25 ± 0·77	206·29 ± 1·14	20·96 ± 1·32**
	♂	173·21 ± 1·24	168·71 ± 2·11	4·50 ± 2·60*	198·06 ± 0·79	178·80 ± 0·85	19·26 ± 1·17**
Sternopleural chaetae (number)	♀	21·06 ± 0·24	19·26 ± 0·37	1·80 ± 0·46*	19·57 ± 0·22	17·41 ± 0·20	2·16 ± 0·31**
	♂	19·34 ± 0·25	17·73 ± 0·37	1·61 ± 0·46*	18·44 ± 0·22	16·24 ± 0·21	2·20 ± 0·32**
Abdominal chaetae (number)	♀	41·37 ± 0·68	39:10 ± 0·68	2·27 ± 0·97*	43·23 ± 0·29	39·32 ± 0·46	3·91 ± 0·52**
	♂	32·45 ± 0·60	31·77 ± 0·62	0·68 ± 0·87	35·47 ± 0·30	31·42 ± 0·31	4·05 ± 0·44**
Ovarioles (number)	♀	37·96 ± 0·94	33·13 ± 0·79	4·83 ± 1·21**	47·57 ± 0·45	38·59 ± 0·66	8·98 ± 0·74**
Development (hours)	♀	199·66 ± 3·93	205·69 ± 4·05	−6·03 ± 6·72	208·16 ± 2·06	207·46 ± 1·75	0·70 ± 2·84
	♂	206·26 ± 3·64	210·72 ± 3·91	−4·46 ± 5·43	213·22 ± 2·13	213·27 ± 1·57	−0·05 ± 7·28
Viability	♀+♂	73·97 ± 4·80	70·97 ± 2·85	3·00 ± 5·35	73·43 ± 2·24	67·60 ± 2·61	5·83 ± 3·44

than in European strains and, among 11 calculated differences, 8 are significant at the 0·05 level. These results are similar to those already obtained in *D. melanogaster* (Table 5 and David *et al.* 1977).

Viability and duration of development show only small and non significant differences between French and African strains; in *D. melanogaster* also these physiological traits do not discriminate between tropical and temperate populations.

The contrast between temperate and tropical strains of *D. simulans* can be illustrated by a principal components analysis (fig. 1) on 5 biometrical traits available for both sexes (weight, wing and

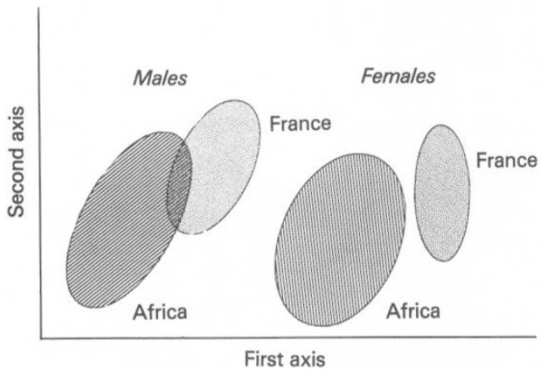

Figure 1 Result of a principal components analysis applied to 5 biometrical traits of French and Afrotropical strains of *Drosophila simulans*. Each ellipse is calculated for including 75 per dent of strains. The two first axes restitute 92 per cent of the total information.

thorax lengths and chaetae numbers). The two first axes constitute 92 per cent of the total variation. The first is mainly correlated to length characters (thorax and wing) and the second to chaetae numbers. Males are clearly separated from females because of their small size and geographic discrimination is better for females than for males.

DISCUSSION

How much polymorphism and geographic differentiation is there in *D. simulans* and how do these data compare to those already obtained from its sibling cosmopolitan species *D. melanogaster*?

Published results on allozyme polymorphism for *D. simulans* are quite diverse. The level of heterozygosity is strongly influenced by the choice of loci and by the number of loci studied. However, if we average the values of Kojima *et al.*, (1970), Steiner *et al.*, (1976), Triantaphyllidis *et al.*, (1980), Cabrera *et al.*, (1982), Onishi *et al.*, (1982) and ourselves, we obtain a mean of 0·12; a proportion of polymorphic loci of 0·44; and an estimate of mean number of alleles per locus of 1·8. These estimates, albeit imprecise are comparable to those found in other organisms (Powell, 1975; Nevo, 1978). *D. simulans* is less variable than are some tropical *Drosophila* species but is not very different in this respect from the average *Drosophila*. An average of these parameters in *D. melanogaster* using the studies of Kojima *et al.*, (1970), Langley *et al.*, (1974), Band (1975), Triantaphyllidis *et al.*, (1980), Cabrera *et al.*, (1982), Onishi *et al.*, (1982), Singh *et al.*, (1982), provides an estimate of 0·15 for $\bar{H}$, of 0·65 for proportion of polymorphic loci, and of 1·8 for the number of alleles per locus. Although these comparisons should be extended to more loci studied with identical techniques in the same laboratory, it does seem that while *D. melanogaster* may have a slightly elevated heterozygosity and a greater proportion of polymorphic loci, neither of the two sibling species are exceptional in this respect within the genus *Drosophila*. If we extend the comparison to single loci, we find that while *D. simulans* is monomorphic or almost monomorphic for loci which are highly polymorphic in *D. melanogaster* (such as ADH, α-GPDH and G6PD) several loci (such as EST-C and ACPH) are more variable in *D. simulans*.

ACPH, ALDOX, EST-6 and HK-1 in *D. simulans* do apparently show some tendency to vary with latitude (although this work needs to be extended by the study of more populations on different continents) and only the EST-6 (Anderson and Oakeshott, 1984) data are at all satisfactory. Genetic distances are smaller between populations living in the same geographic area with the extension of the isolated Seychelles population.

There is a clear contrast between *D. melanogaster* and *D. simulans*: *D. simulans* is far less geographically diversified than is its sibling. Although it is difficult to compare "D" in 2 species with different sets of loci and different geographical patterns of sampling, the average value of D in *D. simulans* is about 4 times lower than in *D. melanogaster* (Singh *et al.*, 1982) (see fig. 2). The genes studied in *D. simulans* are a subset of those studied in *D. melanogaster* and its populations were sampled from much less diverse places. However, the lower variability of *D. simulans* is confirmed even if we consider only the case of single loci and examine the values of their fixation index. In *D. melanogaster*, 17 loci out of 25 had values superior to 0·1 and the average was 0·164 (Singh *et al.*, 1982). In *D. simulans* no fixation

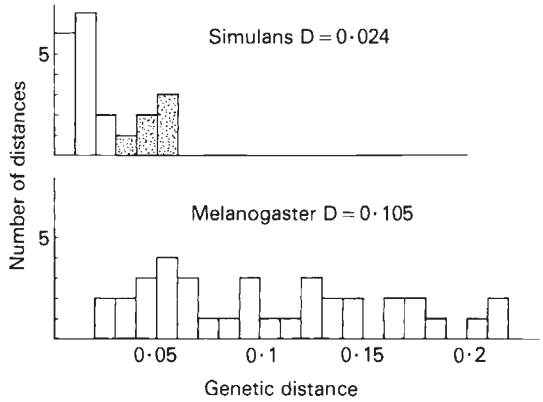

Figure 2 Distribution of genetic distances calculated between geographic populations of *D. simulans* (this work) and *D. melanogaster* (after Singh *et al.*, 1982). D: average value of genetic distance. For *D. simulans*, dotted values correspond to distances including the Seychelles population.

index has a value superior to 0·1 and the average over 10 polymorphic loci gives a value of 0·046. In *D. melanogaster*, the greatest genetic contrast is between Afrotropical and temperate populations (David, 1982; Singh *et al.*, 1982) and nothing analogous exists in *D. simulans*, in spite of the fact that Afrotropical populations are probably ancestral in both species.

There is an increase in average values of morphological traits in European populations of *D. simulans*. The changes concern fresh weight, thorax length, sternopleural and abdominal chaetae numbers, and ovarioles in females, and are similar to those of *D. melanogaster* (table 5). This evolutionary parallelism is illustrated by a discriminant analysis of 6 morphological traits of females (fig. 3).

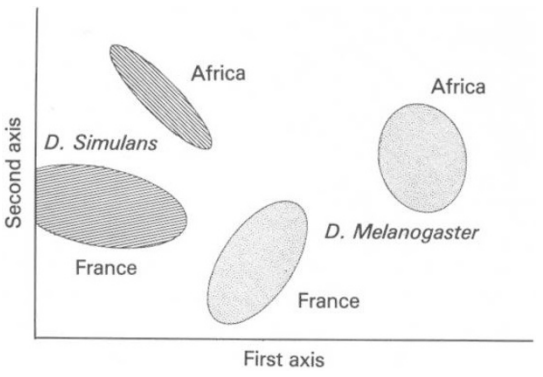

Figure 3 Result of a discriminant analysis applied to 6 biometrical traits of females of *D. melanogaster* and *D. simulans*. Each ellipse includes 75 per cent of strains. The two first axes restitute 99 per cent of the total information.

A direct comparison of phenotypic divergence in the two species is not possible since *D. simulans* is smaller than *D. melanogaster*. We use a relative measure: for each trait, each sex and each species the ratio of the difference to the average value of the trait in French and African populations is calculated. This index is superior for *D. melanogaster* in 10 out of 11 cases. The only exception concerns male weight for which the changes are almost identical in the two species. If we compare these proportions by a simple statistical test, for example Chi square, we get a value of 7·36 with 1 degree of freedom ($p < 0{\cdot}01$). We can conclude that for morphology, *D. simulans* is less geographically variable than is *D. melanogaster*, although the contrast is less pronounced than for allozymes.

D. simulans is monomorphic for chromosome structure, does not exhibit a latitudinal cline for ethanol tolerance and is less variable than *D. melanogaster* for its protein polymorphism measured by 2-dimensional gel electrophoresis. However, there do exist parallel latitudinal clines in the two species in Australia for tolerance to desiccation (Parsons, 1980*b*, *c*), and *D. simulans* from Africa appears to differ from European populations in the composition of cuticular hydrocarbons (Luyten, 1982). In addition pattern of change in mitochondrial DNA suggests that *D. simulans* is divided into three geographic groups, one found in Madagascar, a second in Seychelles, New Caledonia and Hawaii, and a third in the rest of the world (Baba-Aissa and Solignac, 1984).

It was expected 20 years ago (Baker and Stebbins, 1965) that there may be some common genetic properties of colonising species. Our results show that this suggestion is far from true. *D. simulans* and *D. melanogaster* are closely related and are the most efficient colonisers in the genus *Drosophila*. However, the genetic structures of geographic populations are different; for most traits, (including protein polymorphism, chromosome structure, alcohol tolerance and morphology) *D. simulans* is much less differentiated than is *D. melanogaster*. It is not yet known whether the two species do show geographical parallelism in other traits which might result from the action of natural selection.

Acknowledgments We are grateful to Drs D. Lachaise, B. Pintureau, S. Tsakas and J. Vouidibio for providing some *D. simulans* populations as well as to Mrs De Scheemacker-Louis and E. Pla for doing the biometrical measurements.

REFERENCES

ALLEMAND, R. AND DAVID, J. R. 1976. The circadian rhythm of oviposition in *Drosophila melanogaster*: A genetic latitudinal cline in wild populations. *Experientia, 32*, 1403–1404.

ANDERSON, P. R. AND OAKESHOTT, J. C., 1984. Parallel geographical pattern of allozyme variation in two sibling *Drosophila* species. *Nature, 308*, 729–731.

ASHBURNER, M. AND LEMEUNIER, F. 1976. Relationship within the *melanogaster* species subgroup of the genus *Drosophila* (Sophophora). I. Inversion polymorphisms in *Drosophila melanogaster* and *D. simulans. Proc. R. Soc. Lond. B, 193*, 137–159.

AYALA, F. J., POWELL, R., TRACEY, M. L., MOURA, C. A. AND PEREZ-SALAS, S. 1972. Enzyme variability on the *D. willistoni* group. IV. Genic variation in natural populations of *D. willistoni. Genetics, 71*, 113–139.

BABA-AISSA, F. AND SOLIGNAC, M. 1984. La plupart des populations actulles de *Drosophila simulans* ont probablement pour ancêtre une femelle unique dans un passé récent. *C.R. Acad. Sci. Paris. 299*, 289–292.

BAKER, H. G. AND STEBBINS, G. L. 1965. The genetics of colonizing species. New York, Acad. Press, 588 pp.

BAND, H. T. 1975. A survey of isozyme polymorphism in a *Drosophila melanogaster* natural populations. *Genetics, 80*, 761–771.

BERGER, E. M. 1970. A comparison of gene-enzyme variation between *Drosophila melanogaster* and *D. simulans. Genetics, 66*, 677–683.

BOULETREAU-MERLE, J., ALLEMAND, R., COHET Y. AND DAVID, J. R. 1982. Reproductive strategy in *Drosophila melanogaster*: significance of a genetic divergence between temperate and tropical populations. *Oecologia, 53*, 323–324.

CABRERA, V. M., GONZALEZ, A. M., LARRAGA, J. M. AND GULLON, A. 1982. Electrophoretic variability in natural populations of *Drosophila melanogaster* and *D. simulans. Genetica, 59*, 191–201.

CAPY, P., DAVID, J. R., ALLEMAND, R., HYYTIA, P. AND ROUAULT, J. 1983. Genetic properties of North African *Drosophila melanogaster* and comparison with European and Afrotropical populations. *Genet. Sel. Evol., 15* (2), 185–200.

COHET, Y., VOUIDIBIO, J. AND DAVID, J. R. 1980. Thermal tolerance and geographic distribution: a comparison of cosmopolitan and tropical endemic *Drosophila* species. *J. Therm. Biol., 5*, 69–74.

DAVID, J. R. 1974. Utilization of morphological traits for the analysis of genetic variability in wild populations. *Aquilo, Ser. Zool., 20*, 49–61.

DAVID, J. R. 1982. Latitudinal variability of *Drosophila melanogaster*: Allozyme frequencies divergence between European and Afrotropical populations. *Biochemical Genetics, 20*, 7/8, 747–761.

DAVID, J. R. AND BOCQUET, C. 1975. Similarities and differences in latitudinal adaptation of two *Drosophila* sibling species. *Nature, 257*, 588–590.

DAVID, J. R., BOCQUET, C. AND PLA, E. 1976. New results on the genetic characteristics of the Far East race of *Drosophila melanogaster. Genet. Res. Camb., 28*, 253–260.

DAVID, J. R., BOCQUET, C. AND DE SCHEEMAEKER-LOUIS, M. 1977. Genetic latitudinal adaptation of *Drosophila melanogaster*: New discriminative biometrical traits between European and Equatorial African populations. *Genet. Res. Camb., 30*, 247–255.

DAVID, J. R. AND TSACAS, L. 1981. Cosmopolitan, subcosmopolitan and widespread species: Different strategies within the Drosophilid family (Diptera). *C.R. Soc. biogeog., 57*, 11–26.

KIMURA, M. 1983. *The Neutral Theory of Molecular Evolution.* Cambridge Univ. Press, Cambr., 367 pp.

KNIBB, W. R. 1982. Chromosome inversion polymorphisms in *Drosophila melanogaster.* II. Geographic clines and climatic associations in Australasia, North America and Asia. *Genetica, 58*, 213–221.

KNIBB, W. R., OAKESHOTT, J. L. AND GIBSON, J. R. 1981. Chromosome inversion polymorphism in *Drosophila melanogaster.* I. Latitudinal clines and associations between inversions in Australian populations. *Genetics, 98*, 833–847.

KOJIMA, K. I., GILLESPIE, J. AND TOBARI, Y. N. 1970. A profile of *Drosophila* species enzymes assayed by electrophoresis. I. Number of alleles, heterozygosities, and linkage disequilibrium in Glucose-metabolizing systems and some other enzymes. *Biochem. Genet., 4*, 627–637.

LAKOVAARA, S. AND KERANEN, L. 1980. Variation at the α-gpdh locus of Drosophilids. *Hereditas, 92*, 251–258.

LANGLEY, C. H., TOBARI, Y. N. AND KOJIMA, K. I. 1974. Linkage disequilibrium in natural populations of *Drosophila melanogaster.* Genetics, *78*, 921–936.

LEWONTIN, R. C. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. *Amer. Nat., 123*, 115–124.

LUYTEN, I. 1982. Variations intraspécifique et interspécifique des hydrocarbures cuticulaires chez *Drosophila simulans* et des espèces affines. *C.R. Acad. Sci. Paris, 295*, 733–736.

METTLER, L. E., VOELKER, R. A. AND MUKAI, T. 1977. Inversion clines in populations of *Drosophila melanogaster. Genetics, 87*, 169–176.

NEI, M. 1972. Genetic distance between populations. *Am. Nat., 106*, 283–290.

NEVO, E. 1978. Genetic variation in natural populations: patterns and theory. *Theoret. Pop. Biol., 13*, 121–177.

OAKESHOTT, J. G., CHAMBERS, G. K., GIBSON, J. B. AND WILCOKS, D. A. 1981*a*. Latitudinal relationship of esterase-6 and phosphoglucomutase gene frequencies in *Drosophila melanogaster. Heredity, 47* (3), 385–396.

OAKESHOTT, J. G., GIBSON, J. B., ANDERSON, P. R., KNIBB, W. R., ANDERSON, D. G. AND CHAMBERS, G. K. 1981*b*. Alcohol dehydrogenase and Glycerol-3 phosphate dehydrogenase clines in *Drosophila melanogaster* on different continents. *Evolution, 36* (1), 86–96.

O'BRIEN, S. J. AND MACINTYRE, R. J. 1969. An analysis of gene-enzyme variability in natural populations of *Drosophila melanogaster* and *D. simulans. Am. Nat., 103*, 97–113.

ONISHI, S., LEIGH BROWN, A. J., VOELKER, R. A. AND LANGLEY, C. H. 1982. Estimation of genetic variability in natural populations of *D. simulans* by two dimensional and starch gel electrophoresis. *Genetics, 100*, 127–136.

PARSONS, P. A. 1975. The comparative evolutionary biology of the sibling species. *Drosophila melanogaster* and *D. simulans. Quat. Rev. Biol., 50*, 151–169.

PARSONS, P. A. 1980*a*. Isofemale strains and evolutionary strategies in natural populations. *Evolutionary Biology, 13*, 175–217.

PARSONS, P. A. 1980*b*. Parallel climatic races for tolerances to high temperature desiccation stress in two *Drosophila* species. *J. Biogeog., 7*, 97–101.

PARSONS, P. A. 1980*c*. Adaptative strategies in natural populations of *Drosophila*: Ethanol tolerance, desiccation resistance and development times in climatically optimal and extreme environments. *Theor. Appl. Genet., 57*, 257–266.

PARSONS, P. A. 1983. *The Evolutionary Biology of Colonizing Species.* Cambridge Univ. Press, Cambridge, 262 pp.

PARSONS, P. A. AND STANLEY, S. M. 1981. Domesticated and widespread species. Ashburner, M., Carson, H. L. and Thompson, J. N. Jr., (eds.) *The Genetics and Biology of Drosophila*, Vol. 3a, Acad. Press, New York, pp. 349-393.

POWELL, J. R. 1975. Protein variation in natural populations of animals. *Evolut. Biol.*, *8*, 79-119.

SALAM, E. A., EL-ADL, A. M. AND KOSBA, Z. A. 1981. Isozyme polymorphism in *Drosophila*. IV. Interspecific variation and population dynamics. *Proc. 7th Europ. Drosoph. Conf.*, Oulu-Finland, pp. 227-235.

SHOW, C. R. AND PRASAD, R. 1970. Starch gel-electrophoresis of enzymes. A compilation of recipes. *Biochem. Genet.*, *4*, 297-320.

SINGH, R. A., HICKEY, D. A. AND DAVID, J. R. 1982. Genetic differentiation between geographically distant populations of *Drosophila melanogaster*. Genetics, *101*, 235-256.

STALKER, H. D. 1980. Chromosome studies on wild populations of *Drosophila melanogaster*. II. Relationship of inversion frequencies to latitude, season, wing-loading and flight activity. *Genetics*, *95*, 211-223.

STEINER, W. W., SANY, K. L. AND PAIK, Y. 1976. Electrophoretic variability in island population of *Drosophila simulans* and *D. immigrans*. *Biochem. Genet.*, *14*, 495-506.

TANTAWY, A. O. AND MALLAH, G. S. 1961. Studies on natural populations of *Drosophila*. 1. Heat resistance and geographic variation *Drosophila melanogaster* and *D. simulans*. *Evolution*, *15*, 1-14.

TEISSIER, G. 1957. Discriminative biometrical characters in French and Japanese *Drosophila melanogaster*. *Proc. Int. Genet. Symp. Tokyo-Kyoto.* 1956. Cytologia suppl., 502-505.

TRIANTAPHYLLIDIS, C. D. 1973. Allozyme variation in populations of *Drosophila melanogaster* and *D. simulans* from Northern Greece. *J. Heredity*, *64*, 69-72.

TRIANTAPHYLLIDIS, C. D., SCOURAS, Z. G., PANOURGIAS, J. N. AND IOANNIDIS, G. C. 1982. Allozyme variation in Greek wild populations of *Drosophila melanogaster* and *D. simulans* along a North-South gradient. *Genetica*, *58*, 129-136.

TRIANTAPHYLLIDIS, C. D., PANOURGIAS, J. N., SCOURAS, J. G. AND IOANNIDIS, G. C. 1980. A comparison of gene-enzyme variation between *Drosophila melanogaster* and *Drosophila simulans*. *Genetica*, *51*, 227-231.

TSACAS, L. AND LACHAISE, D. 1974. Quatre nouvelles espèces de la Côte-d'Ivoire du genre *Drosophila*, groupe *Melanogaster* et discussion de l'origine du sous-groupe *melanogaster* (Diptera; Drosophilidae). *Ann. Univ. Abidjan, Ser. E.* (*Ecol.*), *7*, 193-211.

VOELKER, R. A., COCKERHAM, C. C., JOHNSON, F. M., SCHAFFER, H. E., MUKAI, T. AND METTLER, L. E. 1978. Inversions fail to account for allozyme clines. *Genetics*, *88*, 515-527.

VOELKER, R. A., MUKAI, T. AND JOHNSON, F. M. 1977. Genetic variation in populations of *Drosophila melanogaster* from the Western United States. *Genetica*, *47*, 143-148.

WATANABE, T. K. AND WATANABE, T. 1977. Enzyme and chromosome polymorphism in Japanese natural populations of *Drosophila melanogaster*. *Genetics*, *85*, 319-329.

WHEELER, M. R. 1981. The drosophilidae: a taxonomic overview. Ashburner, M., Carson, H. L. and Thompson, J. N. Jr. (eds.) *The Genetics and Biology of Drosophila*, Vol. 3a, Academic Press, New York, pp. 1-121.