# Allozyme polymorphism in populations of *Ceratitis capitata* from Algeria, the northwestern Mediterranean coast and Reunion Island

Salah Oukil<sup>a,b\*</sup>, Robert Bues<sup>b</sup>, Jean-François Toubon<sup>b</sup>, Serge Quilici<sup>c</sup>

<sup>a</sup> SRPV d'Alger, 12 avenue Hacène Badi, BP 80, El-Harrach, Alger, Algeria

<sup>b</sup> UMR Inra/UAPV, Écologie des invertébrés, 84914 Avignon Cedex 9, France

<sup>c</sup> Cirad-flhor, BP 180, 97455 Saint-Pierre, île de la Réunion, France

# Allozyme polymorphism in populations of *Ceratitis capitata* from Algeria, the northwestern Mediterranean coast and Reunion Island.

Abstract — Introduction. In Algeria, the Mediterranean fruit fly Ceratitis capitata Wiedmann constitutes the main obstacle to production and exportation of many fruits. In studies of the genetic structure differences of medfly populations, certain authors, using molecular markers, observed the existence of different patterns among the pest Mediterranean populations. A clear understanding of the source and migration of the Mediterranean fruit fly would be useful for undertaking a successful eradication or control program. For this reason, preliminary work sought to compare the genetic structure of Algerian populations of C. capitata with that of other populations situated either in the western Indian ocean or on the northwestern Mediterranean coast. Materials and methods. The study of enzyme polymorphism allowed the comparison of the genetic structure of four Algerian populations of Ceratitis capitata with one from Reunion Island and five other populations collected from the northwestern Mediterranean coast (France and Spain). Enzyme analyses were performed on ground pest adults electrophoresed on a starch gel. Fifteen loci were analyzed for each population. Results and discussion. In spite of a wide geographic distribution of the analyzed populations (from a latitude of 24° to 44° N), no gradient of allelic frequencies was observed for any of the polymorphic loci. A higher genetic variability was observed in the population of Reunion Island than in the populations of Algeria or the northwestern Mediterranean coast. No genetic differentiation was observed among the populations of southern Algeria (Djanet and Ghardaïa) and northern Algeria (Boufarik and Oran).

Algeria / France / Spain / Reunion / *Ceratitis capitata* / fruit damaging insects / enzyme polymorphism

# Polymorphisme enzymatique de populations de *Ceratitis capitata* originaires d'Algérie, du littoral nord-ouest méditerranéen et de l'île de la Réunion.

Résumé — Introduction. En Algérie, la mouche méditerranéenne des fruits, Ceratitis capitata, est le principal obstacle à la production et l'exportation de fruits. En étudiant les différences de structures génétiques entre populations de mouches des fruits à partir de marqueurs moléculaires, certains auteurs ont observé l'existence de comportements différents parmi les populations méditerranéennes du ravageur. Une bonne compréhension de l'origine et de la migration de l'insecte serait utile pour entreprendre son éradication ou adopter des mesures de contrôle. Pour cette raison, des travaux préliminaires ont cherché à comparer la structure génétique de populations algériennes de *C. capitata* avec celle d'autres populations localisées ou dans l'ouest de l'océan Indien, ou sur le littoral nord-ouest de la Méditerranée. **Matériel** et méthodes. L'étude du polymorphisme enzymatique de C. capitata a permis de comparer la structure génétique de quatre populations d'Algérie avec celle de l'île de la Réunion et cinq autres populations prélevées sur la côte nord-ouest de la Méditerranée (France et Espagne). Des analyses d'enzymes ont été effectuées sur des broyats d'insectes adultes étudiés par électrophorèse sur gels d'amidon. Quinze loci ont été analysés pour chaque population. Résultats **et discussion**. Malgré la large distribution géographique des populations analysées (lat. 24° à 42° N), aucun gradient des loci polymorphes n'est apparu. Une plus forte variabilité génétique a été observée pour la population de l'île de la Réunion que pour celles localisées en Algérie ou sur la côte nord-ouest de la Méditerranée. Il n'existe pas de différentiation génétique entre les populations isolées du sud de l'Algérie (Djanet et Ghardaïa) et celles situées au nord (Boufarik et Oran).

Algérie / France / Espagne / Réunion / *Ceratitis capitata* / insecte déprédateur des fruits / polymorphisme enzymatique

\* Correspondence and reprints

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### 1. Introduction

In Algeria, the Mediterranean fruit fly *Ceratitis capitata* Wiedmann constitutes the main obstacle to the fruit production and the exportation of citrus, apricots and peaches. The introduction of *C. capitata* to the Mediterranean basin was believed to have occurred in 1842 [1]. Medflies were reported for the first time in the surroundings of Algiers in 1859. This insect was found in the wasteland and oases where climatic conditions and a diversification of fruit species are favorable for its proliferation.

Many authors have studied the population variability of *C. capitata* throughout its vast geographic distribution area. Huettel *et al.* [2] were the first, as far as we know, to have studied the genetic structure differences using enzymatic protein electrophoresis. These authors found a higher genetic variability in a South African population than in a population from Israel.

Subsequently, researchers [3-5] worked on the hypothesis that the ancestral populations of South Africa, Kenva and Reunion Island have a higher enzyme polymorphism than that observed in the populations collected in the Mediterranean basin. These populations might have been introduced in small numbers and their present genetic structure might have resulted from a founder effect. Under this hypothesis, the Sahara was supposed to constitute a geographic bottleneck to the dispersion of genes originating from ancestral populations. Gasparich et al. [6], in their study of several populations of the Mediterranean basin using molecular markers, observed in the population of Tozeur, in the south of Tunisia, the existence of a pattern different from the other Mediterranean populations.

Algeria has a Sahara geographical area extending from the latitude  $37^{\circ}$  to  $19^{\circ}$  N, including scattered oases. A clear understanding of the source and migration of the Mediterranean fruit fly would be useful for undertaking a successful eradication or control program. For this reason, preliminary work sought to first compare the genetic structure of the South-Algerian populations of *C. capitata* with that of a population of Reunion Island situated in the western Indian ocean and, secondly, the populations collected on the northwestern Mediterranean coast (Spain and France) and in the Island of Corsica with that of populations of coastal Algeria.

### 2. Materials and methods

#### 2.1. Origin of samples

Samples were taken from ten localities on different host plants (*table I*). Pupae were then collected, and the obtained adults were frozen at -80 °C. Nevertheless, strains of unknown origin, kept for many years in the laboratory, were also analyzed. For these samples, the allelic frequencies were shown for comparison with natural populations, but they were not taken into account in the analysis of results.

#### 2.2. Electrophoretic studies

The adults were ground in 30  $\mu$ L of trisborate-EDTA buffer (pH 7) and were then analyzed on horizontal gels of starch. Fifteen enzyme loci of each population were analyzed with the exception of the localities of Ghardaïa and Oran (Algeria), for which only the polymorphic loci were analyzed. The buffers used were:

- tris-lithium-citrate-borate buffer (pH 8,3) for aconitase hydratase (*Acoh*), alcohol dehydrogenase (*Adh*), malic enzyme (*Me*), glucose-6-phosphate-isomerase (*Gpi*), hexokinase (*Hk*), leucine-amino-peptidase (*Lap*) and phosphogluconate dehydrogenase (*Pgdh*);

- tris-maleate buffer (pH 7,3) for aspartate aminotransferase (*Aat*), adenylate kinase (*Ak*), 3-hydroxybutyrate dehydrogenase (*Hbdh*), isocitrate dehydrogenase (*Idh*), 1-lactate dehydrogenase (*Ldh*), malate dehydrogenase (*Mdh*), phosphoglucomutase (*Pgm*) and alpha glycerophosphate dehydrogenase (*Gpdh*).

The analysis of manose-6-phosphate isomerase (*Mpi*) and esterase (*Est*) was abandoned because of illegibility. Electrophoretic and staining procedures were

#### Table I.

Locations, dates of sampling and host plants of *Ceratitis capitata* populations from ten localities of Algeria, France and Spain.

Country	Locality	Latitude	Date	Host plant		
Algeria	Boufarik	36° 2'	June 1993	Apricot		
	Djanet	24° 0'	July 1996	Bitter orange		
	Ghardaïa	32° 5'	February 1996	Bitter orange		
	Oran	35° 8'	May 1997	Apricot		
France	Avignon	44° 1'	October 1991	Apple		
	Montpellier	43° 7'	October 1991	Apple		
	Perpignan	43° 1'	November 1991	Apple		
	Corsica	42° 1'	December 1992	Persimmon		
	Reunion <sup>a</sup>	21° 2'	July 1999	Murraya paniculata		
Spain	Gerone	41° 9'	June 1992	Orange		
<sup>a</sup> Southern Hemisphere.						

carried out according to Pasteur *et al.* [7] and Hillis and Moritz [8].

For each locality, 24 to 96 individuals were analyzed. As the allele frequencies did not differ between females and males, the allele frequencies of the sexes were grouped together.

#### 2.3. Data analysis

The deviations from Hardy-Weinberg expectations were analyzed with the test described by Louis and Dempster [9]. The F statistics were calculated according to the formula of Weir and Cockerham [10]. The standard deviations and the confidence intervals were assessed by the methods of Jackknife and Bootstrap on loci, respectively. Linkage disequilibrium between loci was not calculated because the enzymatic systems were not analyzed on the same individual. The allelic frequencies were compared per locus with the exact test of Fisher and the global test was calculated by the method of Fisher [11] (for this test, each locus is considered to be independent).

Different population groups were pooled according to their geographic distribution. In these cases, individuals were grouped together before the calculation of frequencies. The average number of individuals exchanged between populations at each generation were calculated according to the pattern described by Wright [12]. In this pattern, the gene flow between populations was determined by the number of migrants, Nm, whose calculation was based on the inverse relation between Nm and Fst (which measures the genetic difference between populations): Nm = [(1 / Fst - 1) /4]. Another method to calculate Nm [13]. based on private alleles, establishes a relation between the average frequency of private alleles  $p_{(1)}$  and the gene flow: {log  $[p_{(1)}]$  $= 0.505 \times \log (Nm) - 2.44$ . A correction was used for mean sample size (Ns) by multiplying Nm by (25 / Ns) [14]. These calculations were done with Genepop software [15] and Biosys [16].

#### 3. Results

#### 3.1. Comparison between populations

Five (*Pgm, Aat, Idh, GPI* and *Hbdh*) out of the fifteen loci tested were found to be polymorphic for at least one population (the main allele frequency < 99%) with the exception of the Gerone population for which all the loci tested were found to be monomorphic (*table II*). For the Reunion Island population, four other loci (*Aco, Mdh, Adh* and *Hk*) were found to be polymorphic, but the allele frequencies were uncertain and the loci were not taken into account in the calculations. The level of heterozygosity varied from 0 for Gerone to 0.116 for Oran (*table III*). The breeding laboratory population presented only two polymorphic loci (*Pgm* and *Aat*) and a rate of heterozygosity of 0.076 (*table III*).

In three cases, the analysis per locus and per population gave rise to significant deviation from Hardy-Weinberg expectation: a deficit of heterozygotes in Oran at *Pgm* (P = 0.005), in Reunion Island at *Idh* ( $P \le 0.0000$ ) and a case of an excess of heterozygotes at *Aat* (P = 0.0227) in Oran.

The high values of *Fis* (which measures deviations within populations) and *Fit* (which measures deviations of the whole populations) observed at the locus *Idh* (*table IV*) confirmed the deficit in heterozygotes. The value of average *Fst* was 0.0397 with a standard deviation of 0.008 and the confidence limits of 0.0146 to 0.0476. The genetic differentiation between populations was significant at the 1% threshold for *Pgm, Idh* and *Aat* and the inter-loci test was highly significant.

The number of migrants (*Nm*), calculated by the *Fst* estimation [10], was 6. This value was 4 when calculated by the Slatkin method [13], with one mean private allele frequency of 0.026. Three private alleles were observed in the Reunion Island population at the *Pgm*, *Idh* and *Pgi* loci, with respective percentages of (4.2, 4.7 and 1)% and one private allele in the Boufarik population at *Hbdh* (0.5%).

# 3.2. Comparison of populations by geographic zones

There was a significant genetic differentiation between the five populations collected in France (Perpignan, Montpellier, Avignon and Corsica) and Spain (Gerone) (P = 0.0005) (*table V*). The differentiation disappeared when the Montpellier population was not taken into account (P = 0.1151). The four populations of Algeria (Djanet, Ghardaïa, Boufarik and Oran) were significantly different genetically (P = 0.0039), but the populations of Djanet, Ghardaia and Boufarik alone were not significantly different (P = 0.5003).

The two populations of Montpellier and Oran shared a high percentage of the same allele at the *Pgm* locus, other than the majority allele, respectively (17 and 18.8)% (*table II*). Nevertheless, in one case (Oran), a high proportion of this allele was brought by homozygote individuals whereas in the other (Montpellier) no homozygotes were observed. These two populations were not significantly different (P = 0.4323).

Without the populations of Oran and Montpellier, the comparison of the seven remaining populations presented no significant differences (P = 0.0975, *table V*).

Comparisons performed on allele frequencies of the Reunion Island population with the populations of Spain and France (without Montpellier) and of Algeria (without Oran) proved highly significant ( $P \le 0.000$ ).

For all comparisons, the *Fst* value was relatively low (*table V*) and *Nm* values, calculated by the *Fst*, from 5 to 22.

## 4. Discussion

Like many other authors [3, 4], we observed a higher enzyme variability in the population of Reunion Island than in those of Algeria and the northwestern Mediterranean coast (France and Spain). Nevertheless, in the studies conducted with a molecular marker (mitochondrial DNA) [6], there did not seem to be a genetic differentiation between the isolated populations of the South (Djanet and Ghardaïa) and the population of North Algeria (Boufarik). This result could be explained either by the numerous fruit and vegetable exchanges between the different regions or by the effect of winds [17]. However, in the Oran population, we observed a high percentage of an allele at the Pgm locus which makes it possible to distinguish it from the other three Algerian populations. This characteristic was also

Locality	Number of	-	Pgm			HbdH			ldh		Aá	at		Pgi	
	observed individuals	<del></del>	2	ę	-	2	e	-	0	с	-	2	-	0	ę
Avignon	24 to 48	0.000	0.969	0.031	0.000	1.000	0.000	0.000	1.000	0.000	0.014	0.986	0.000	1.000	0.000
Boufarik	96 to 120	0.000	0.906	0.094	0.005	0.990	0.005	0.004	0.996	0.000	0.021	0.979	0.000	1.000	0.000
Corsica	24 to 39	0.000	0.979	0.021	0.000	1.000	0.000	0.000	1.000	0.000	0.021	0.979	0.021	0.979	0.000
Djanet	31 to 39	0.000	0.936	0.064	0.000	1.000	0.000	0.000	1.000	0.000	0.026	0.974	0.026	0.974	0.000
Gerone	24	0.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000	1.000	0.000
Ghardaïa	31 to 48	0.000	0.984	0.016	0.000	1.000	0.000	0.000	1.000	0.000	0.016	0.984	0.000	1.000	0.000
Montpellie	- 24 to 47	0.000	0.830	0.170	0.000	1.000	0.000	0.000	1.000	0.000	0.014	0.986	0.021	0.979	0.000
Oran	96	0.000	0.813	0.188	0.000	1.000	0.000	0.000	1.000	0.000	0.083	0.917	0.063	0.937	0.000
Perpignan	24 to 48	0.000	0.917	0.083	0.000	1.000	0.000	0.000	1.000	0.000	0.073	0.927	0.042	0.958	0.000
Reunion	192	0.042	0.943	0.016	0.000	0.974	0.026	0.068	0.885	0.047	0.000	1.000	0.010	0.979	0.011
Pgm: phos	phoglucomu	ıtase, <i>Hb</i> a	<i>th:</i> 3-hydrc	xybutyrate	e dehydrog	jenase, <i>Id</i> .	h: isocitrate	ehydrog	lenase, <i>Aa</i>	<i>it:</i> aspartat	e aminotra	nsferase, <i>H</i>	<i>gi:</i> phosph	iogluco-is	omerase.
Table III. Heterozy	gosity unb	iased an	nd total p	ercentag	jes for ea	ach locus	s of the fr	equencie	es of alle	les other	than the	majority	allele for	populat	ions
of Cerati	tis capitata	a sample	d in ten	localities	of Algeri	ia, Franc	e and Sp	ain. Data	a on a lat	ooratory :	strain are	e presente	ed for co	npariso	<i>.</i> -
Locality		Heten	ozygosity		Ρg	m	Hbα	ţ		ldh		Aat		Pgi	
Avignon		0	0.018		Ċ,	<del>, ,</del>	0.0			0.0		4.		0.0	
Correico		50	).048 0.055		ດີດ	4	1.0			4.0		2.1 1		0.0	
Djanet		0	0.045		10	4	0.0			0.0		2.6		2.6	
Ghardaïa		0	0.013		4.	9	0.0			0.0		1.6		0.0	
Gerone		00	0000		1 O	0,0	0.0			0.0		0.0		0.0	
Pernichemen			1.075		2 00		0.0			0.0		7 - 4		4.1	
Oran		0	0.116		18.	οœ	0.0			0.0		8.3		6.3	
Reunion		0	0.082		5.	8	2.6			11.5		0.0		2.1	
Laboratory	strain	0	0.076		12.	2	0.0			0.0		8.3		0.0	

Pgm: phosphoglucomutase, Hbdh: 3-hydroxybutyrate dehydrogenase, Idh: isocitrate dehydrogenase, Aat: aspartate aminotransferase, Pgi: phosphogluco-isomerase.

#### Table IV.

Homogeneity tests of allele frequencies and F-statistic for each of five polymorphic loci for ten populations of *Ceratitis capitata* of different origin.

Locus	Fis	Fit	Fst	P <sup>a</sup>
Pgm	0.0851	0.1250	0.0428	< 0.0000
Hbdh	-0.0177	-0.0061	0.0116	0.1617
Idh	0.9834	1.0478	0.1262	< 0.0000
Aat	0.1412	0.1623	0.0235	0.0036
Pgi	-0.0323	-0.0144	0.0176	0.0121
Mean	0.1572	0.1224	0.0397	< 0.0000 <sup>b</sup>
Standard deviation <sup>c</sup>	0.0814	0.0834	0.0080	
Confidence limit <sup>d</sup> +	0.3392	0.3696	0.0476	
Confidence limit <sup>d</sup> –	0.0255	0.0406	0.0146	

<sup>a</sup> Values of Fisher exact test for significant deviations of *Fst* values from 0.

<sup>b</sup> All loci combined.

<sup>c</sup> Assessed by the methods of Jackknife on loci.

<sup>d</sup> Assessed by the methods of Bootstrap on loci.

*Fis*, *Fit* and *Fst*: measure the deviations within populations, the deviations of the whole populations and the genetic difference between populations, respectively.

#### Table V.

Level of significance of the differences in allele frequencies between geographical areas for each of five polymorphic loci for ten populations of *Ceratitis capitata* of different origin. Values of genetic differentiation (*Fst*) and gene flow (*Nm*).

Loci	France-Spain (5 populations)	Algeria (4 populations)	France-Spain – Algeria <sup>cd</sup> (7 populations)	Populations pooled: France-Spain <sup>c</sup> Algeria <sup>d</sup> Reunion (1 population)
Pgm	0.0001	0.0111	0.0544	0.0122
Hbdh	_	1.0000	1.0000	0.0050
Idh	-	1.0000	1.0000	< 0.0000
Aat	0.0602	0.0736	0.1106	0.0290
Pgi	0.7889	0.0029	0.0537	0.2615
All loci	0.0005 <sup>a</sup>	0.0039 <sup>b</sup>	0.0975	< 0.0000
Genetic differentiation (Fst)	0.0460	0.0306	0.0113	0.0293
Gene flow (Nm)	5.2	7.9	21.9	8.3

<sup>a</sup> If one excludes the Montpellier population the test is no longer significant (P = 0.1151, Fst = 0.0161).

<sup>b</sup> If one excludes the Oran population the test is no longer significant, (P = 0.5003, Fst = 0.0063). The two populations of Montpellier and Oran do not differ genetically (P = 0.4323, Fst = 0.0003).

<sup>c</sup> The populations of France and Spain without the Montpellier population.

<sup>d</sup> The populations of Algeria without the Oran population populations, respectively.

observed in the French population of Montpellier and significantly differentiates it from the two other French populations, even though they are not separated by a large geographic distance (100 to 150 km). However, the absence of homozygotes in Montpellier may lead to the assumption that there was a recent introduction. Being unable to survive the hard winter only in the South of France, the medfly is re-introduced every year and its presence is consequently irregular, which may not allow maintenance of the rare alleles. Once again, an important role is played by commercial exchanges between the ports of Oran (Algeria) and Sète (France), situated 50 km west of Montpellier, which can be different from exchanges between the ports of Algeria and Marseille (France), situated 140 km east of Montpellier.

The complete absence of polymorphism in the Gerone population on fifteen tested loci leads to the assumption that it constitutes a residual population introduced in small numbers without any exchanges with other populations surviving hard winters not favourable in this geographic zone [18]. However, this result will have to be confirmed by a more significant sampling of this population.

In contrast, the samples kept for many years in the laboratory have maintained a relatively high percentage of heterozygosity, higher than the percentage of heterozygosity of wild populations. In spite of the insulation of the laboratory strain, the accidental introduction of wild individuals cannot be excluded.

In three populations (the South, centre and East of Spain), eleven out of twentyfive tested loci were polymorphic for all populations [19]. These eleven loci were also analyzed in our study and only three (*Hbdh, Idh* and *Pgm*) were polymorphic in the Algerian and French populations. In six Mediterranean populations, six out of twenty-five tested loci were polymorphic [20]. In two populations collected in the Southern Hemisphere (Kenya and Reunion Island), twenty-two out of the twenty-five loci tested were found to be polymorphic [3]. This percentage of polymorphism is distinctly higher than that observed in our study on the Reunion Island population even if the four polymorphic loci with uncertain frequencies are taken into account (= nine polymorphic loci out of the fifteen loci tested).

The percentage of polymorphism varied according to the populations; however, it seems that, for a given locality, it could vary slightly according to the host plant on which the population was collected [21]. The comparison of allelic frequencies between samples collected on peaches and bitter orange in Ghardaïa showed no differences. Kourti and Hatzopoulos [20] found a latitudinal cline of allele frequencies for two loci (*G-6-Pdh* and *Idh*). In our study, notwithstanding the large geographic distribution of the populations analyzed (from a latitude of 24° to 44° N), no gradient in allele frequencies was observed for any polymorphic locus.

The average value of Fst obtained from the ten populations for the polymorphic loci (0.0397) was significantly different from 0 and distinctly lower than the results obtained by Gasperi *et al.* [3] (*Fst* = 0.123), calculated from four populations (Reunion Island, Kenya and the two Mediterranean islands of Procida and Sardinia). The values of Nm as calculated between all populations by the methods of Wright or Slatkin were respectively 4 and 6. The theoretical gene flow was substantial (> 1), in agreement with the low genetic differentiation observed. It is very difficult to compare these results with those obtained by Gasperi et al. [3] (1.8 and 0.3, respectively) on four populations, including two from the original zone of the species.

Enzymatic protein electrophoresis has a major disadvantage in that it reveals only one part of the variability. It is possible that sampling, also, does not represent the whole population and that some rare alleles cannot be detected. Dealing with the same set of Mediterranean populations, most of the authors here mentioned have found different polymorphic loci. These different results could be explained by the electrophoretic procedures carried out. The similarity between allele frequencies observed in the populations of South and North Algeria shows the importance of commercial exchanges that counterbalance the effects of genetic drift caused by environmental conditions. Parallel studies with molecular markers [22] and ecophysiological adaptative criteria (thermal threshold of development, resistance to low temperatures) could offer a better understanding of the geographic variability of the species.

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## References

- De Breme F., Note sur le genre *Ceratitis* de M. Mac Leay (Diptera), Ann. Soc. Entomol. Fr. 11 (1842) 183–190.
- [2] Huettel M., Fuerst P.A., Maruyama M., Chakraborty R., Genetic effects of multiple population bottlenecks in the Mediterranean fruit fly (*Ceratitis capitata*), Genetics 94 (1980) 47–48.
- [3] Gasperi G., Guglielmino C.R., Malacrida A.R., Milani R., Genetic variability and gene flow in geographical populations of *Ceratitis capitata* (Wied.) (medfly), Heredity 67 (1991) 347–356.
- [4] Malacrida A.R., Guglielmino C.R., Gasperi G., Baruffi L., Milani R., Spatial and temporal differentiation in colonizing populations of *Ceratitis capitata*, Heredity 69 (1992) 101–111.
- [5] Kourti A., Loukas M., Sourdis J., Dispersion pattern of the medfly from its geographic centre of origin and genetic relationships of the medfly with two close relatives, Entomol. Exp. Appl. 63 (1992) 63–69.
- [6] Gasparich G.E., Silva J.G., Han H.-Y., McPheron B.A., Steck G.J., Sheppard W.S., Population genetic structure of Mediterranean fruit fly (Diptera: Tephritidae) and implications for worldwide colonisation patterns, Ann. Entomol. Soc. Am. 90 (1997) 790–797.
- [7] Pasteur N., Pasteur G., Bonhomme F., Catalan J., Britton-Davidian J., Manuel technique de génétique par électrophorèse des protéines, Lavoisier, Paris, France, 1987, 217 p.
- [8] Hillis D.M., Moritz C., Molecular Systematics, Sinauer Associates, Inc., Sunderland, MA, USA, 1990, 588 p.

- [9] Louis E.J., Dempster E.R., An exact test for Hardy-Weinberg and multiple allele, Biometrics 43 (1987) 805–811.
- [10] Weir B.S., Cockerham C.C., Estimating Fstatistics for the analysis of population structure, Evolution 38 (1984) 1358–1370.
- [11] Fisher R.A., Statistical methods for research workers, 7th ed., Oliver and Boyd, Edinburgh, UK, 1938.
- [12] Wright S., The genetical structure of populations, Ann. Eugenic. 15 (1951) 323–354.
- [13] Slatkin M., Rare alleles as indicators of gene flow, Evolution 39 (1985) 53–65.
- [14] Barton N.H., Slatkin M., A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population, Heredity 56 (1986) 409–415.
- [15] Raymond M., Rousset F., GENEPOP (Version 2): Population genetics software for exact tests and ecumenicism, J. Hered. 86 (1995) 248–249.
- [16] Swofford D.L., Selander R.B., BIOSYS-1: a Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics, J. Hered. 72 (1989) 281–283.
- [17] Fimiani P., Pest status, Mediterranean region, in: Robinson A.S., Hooper G. (Eds), Fruit flies: their biology, natural enemies and control, Vol. 3A, Elsevier, Amsterdam, The Netherlands, 1989, pp. 37–50.
- [18] Fisher-Colbrie P., Busch-Petersen E., Pest status, temperate Europe and West Asia, in: Robinson A.S., Hooper G. (Eds), Fruit flies: their biology, natural enemies and control, Vol. 3A, Elsevier, Amsterdam, The Netherlands, 1989, pp. 91–100.
- [19] Reyes A., Ochando M.D., Use of molecular markers for detecting the geographical origin of *Ceratitis capitata* (Diptera: Tephritidae) populations, Ann. Entomol. Soc. Am. 91 (1998) 222–227.
- [20] Kourti A., Hatzopoulos P., Latitudinal clines of allelic frequencies in Mediterranean populations of *Ceratitis capitata* (Wiedmann), Genet. Sel. Evol. 27 (1995) 201–210.
- [21] Milani R., Gasperi G., Malacrida A., Biochemical genetics (of *Ceratitis capitata*), in: Robinson A.S., Hooper G. (Eds), Fruit flies: their biology, natural enemies and control, Vol. 3A, Elsevier, Amsterdam, The Netherlands, 1989, pp. 33–56.
- [22] Haymer D.S., McInnis D.O., Arcangeli L., Genetic variation between strains of the Mediterranean fruit fly, *Ceratitis capitata*, detected by DNA fingerprinting, Genome 35 (1992) 528–533.

# Polimorfismo enzimático de poblaciones de *Ceratitis capitata* originarias de Argelia, del litoral noroeste mediterráneo y de la isla de la Reunión.

Resumen — Introducción. En Argelia, la mosca mediterránea de la fruta, Ceratitis capitata, representa el principal obstáculo para la producción y exportación de frutos. Estudiando las diferencias de estructuras genéticas entre poblaciones de moscas de la fruta a partir de marcadores moleculares, algunos autores han observado la existencia de comportamientos diferentes entre las poblaciones mediterráneas de esta plaga. Una buena comprensión del origen y de la migración del insecto sería útil para acometer su erradicación o adoptar medidas de control. Por esta razón, unos estudios preliminares intentaron comparar la estructura genética de poblaciones argelinas de *C. capitata* con la de otras poblaciones localizadas en el oeste del océano Índico o en el litoral noroeste del Mediterráneo. Material y métodos. El estudio del polimorfismo enzimático de C. capitata permitió comparar la estructura genética de cuatro poblaciones de Argelia con la de la isla de la Reunión y cinco poblaciones más, recolectadas en la costa noroeste del Mediterráneo (Francia y España). Se efectuaron análisis de enzimas de trituraciones de insectos adultos estudiados mediante electroforesis en gel de almidón. Se analizaron quince loci por cada población. Resultados y discusión. A pesar de la amplia distribución geográfica de las poblaciones analizadas (lat. 24° a 42° N), no apareció ningún gradiente de los loci polimorfos. Se observó una mayor variabilidad genética en la población de la Reunión que en las de Argelia o las de la costa noroeste mediterránea. No hay diferenciación genética entre las poblaciones aisladas del sur de Argelia (Djanet y Ghardaia) y las del norte (Bufarik y Orán).

Argelia / Francia / España / Reunión / *Ceratitis capitata* / insectos depredadores de los frutos / polimorfismo enzimático

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