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Original article

Developmental temperature and somatic excision rate of *mariner* transposable element in three natural populations of *Drosophila simulans*

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Summary – The temperature effect on the somatic excision rate of an inactive copy (*peach*) of the *mariner* transposable element, inserted in the *white* gene and responsible of the mutation (w^{pch}), was investigated in isofemale lines from 3 natural populations of *D simulans*. The somatic excision rate of the *peach* element was measured by the proportion of mosaic males in the offspring of a test-cross between a wild type male (originating from natural populations) and *white peach* females of a reference strain *(GB1)*. A significant effect of the breeding temperature was detected in 2 out of the 3 populations investigated, *ie* Loua (Congo) and Bordeaux (France). In these 2 populations, the proportion of mosaic males increased with temperature. In the third population (Agadir, Morocco), the proportion of mosaic males was always high whatever the temperature. A slight correlation between the excision rate and the number of *mariner* copies was observed. Finally, this temperature effect may be related to a 14-bp sequence localized in the 5′ inverted repeat of the element showing 50–57% of homology with sequences of heat shock protein promoters.

***Drosophila simulans* / transposable element / *mariner* element / temperature**

Résumé – Température de développement et taux d'excision de l'élément *mariner* dans trois populations naturelles de *Drosophila simulans*. *L'effet de la température sur le taux d'excision somatique d'une copie inactive* (peach) *de l'élément* mariner, *insérée dans le gène* white *et responsable de la mutation* white peach *(*w^{pch}*), a été analysé dans des lignées isofemelles de 3 populations naturelles de* Drosophila simulans. *Le taux d'excision somatique de l'élément* peach *a été mesuré par le pourcentage de mâles ayant des yeux mosaïques dans la descendance des croisements entre mâles issus des populations naturelles et des femelles issues d'une lignée de référence* (GB1). *Un effet de la température a été décelé dans 2 populations (Loua et Bordeaux). Dans les 2 cas, le pourcentage de mâles*

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mosaïques augmente avec la température d'élevage. Dans la troisième population (Agadir), ce pourcentage est toujours élevé quelle que soit la température. Par ailleurs, bien que le taux d'excision de l'élément peach *augmente avec le nombre moyen de copies de l'élément présent dans les différentes populations, une seule corrélation significative au seuil de 5% a été trouvée. Enfin, une séquence de 14 pb, située dans l'inversion répétée en 5' de l'élément, présentant 50 à 57% d'homologie avec des séquences de promoteurs de protéines du choc thermique, pourrait être responsable des effets température détectés.*

Drosophila simulans / élément transposable / élément _mariner_ / température

INTRODUCTION

The genome response to environmental stresses has been investigated in many ways (Hoffmann and Parsons, 1991), and often by considering the mutator effect of various chemicals and radiations. In this context and during recent years, several authors have proposed that an environmental factor, like temperature, could modify the transcription and/or the transposition rate of transposable elements (Strand and McDonald, 1985; Junakovic *et al*, 1986; McDonald *et al*, 1987). On the other hand, populational factors, like inbreeding, could be involved in such a phenomenon. However, although Biémont *et al* (1987, 1990) showed spontaneous mobilization of *copia* and *P* elements in 2 inbred lines, it cannot be assumed that consanguinity was responsible for these movements.

Among the different transposable elements described in *Drosophila*, a temperature effect on the excision and/or transposition rate has been demonstrated in several of them. In the *P–M* system, hybrid dysgenesis, due to the mobility of *P* elements, and transposase production are enhanced at high temperature (Engels, 1989 and references therein). In the *I–R* system, the reactivity of *I* strains is affected by temperature (Picard *et al*, 1977; Bucheton, 1978). Junakovic *et al* (1986) and Ratner *et al* (1992) reported an increase of transposition rate related to temperature for *copia*-like elements and Strand and McDonald (1985) showed an increase of *copia* homologous transcript after a heat shock stress. This phenomenon is not limited to *Drosophila*, but has also been reported in many species like *Antirrhinum majus* for the element *Tam3* (see Coen *et al*, 1989 and references therein), *Saccharomyces cerevisiae* for the element *Ty* (Boeke, 1989) and *Escherichia coli* for the element *Tn3* (Sherratt, 1989). In *Drosophila*, the phenomenon related to transposition, *ie* the phenotypic effects of the transposition/excision, are stimulated when the breeding temperature increases. But, in other organisms and for other transposable elements such as *Ty* and *Tam3*, the transposition was increased at low temperature. For the first type, an interaction with promoters sensitive to temperature could exist while for the second type, it is assumed that a thermal degradation of products involved in the transposition might occur.

For the *mariner* element some temperature effects have already been mentioned by Garza *et al* (1991). Such effects were observed in a *D melanogaster* transformed line in which the germinal excision of the non-autonomous *peach* element was controlled by the active element *Mos1*. In this line, the excision rate varied from 10.7% at 18°C to 26.4% at 29°C. In *D simulans* the same phenomenon was observed

and the germinal excision rate of the *peach* element ranged from 0.2% at 18°C to 3.4% at 25°C.

In the present work, we investigated the temperature effect on the somatic excision rate of an inactive element (the *peach* element inserted in the *white* gene) when induced by active elements present in isofemale lines of 3 natural populations of *D simulans*. The general occurrence of active *mariner* elements was previously reported in these natural populations (Capy *et al*, 1990). A relationship between the average number of copies per line and the level of somatic excision was also analysed. We found a significant temperature effect for 2 of the 3 populations tested and a slightly significant overall correlation between the number of copies and the excision rate. Finally, an analysis of *mariner* sequence in 5′ of the initiation site showed a 14-bp sequence with 50–57% of homology with promoter sequence of several heat shock protein (*hsp*) genes.

MATERIALS AND METHODS

Natural populations and breeding temperature

The 3 populations used in this work came from Loua (Congo), Agadir (Morocco) and Bordeaux (France). Season and average temperature at the time of capture are the following: for Loua, November 1989, at the end of the dry season and the begining of the wet season, the average daily temperature was $\approx$ 26–27°C; for Agadir, spring 1989 with an average daily temperature of 21°C and Bordeaux, autumn 1989, more precisely during the vintage season and an average temperature of 17°C. Flies were caught by attractive fermenting traps or directly by sweeping on natural breeding sites. Isofemale lines were initiated from each population (25 for Loua, 22 for Agadir and 31 for Bordeaux) and < 5 generations were kept at 25°C in the laboratory conditions before their analysis. The isofemale line method was used to keep most of the original variability of the sample and to reduce the selection effect of laboratory conditions (Capy, 1987). The experiments were performed at 3 breeding temperatures: 17, 25 and 29°C.

Somatic excisions

The transposable element *mariner* can be excised either somatically or in the germline. Somatic excisions are phenotypically observed when an active element determines the excision of the non-autonomous element *peach* inserted in the *white* gene (mutation *white peach*, w^{pch}). In this case, flies with mosaic eyes are observed. A mosaic eye is a *white peach* phenotype with 1 or several red spots (see, for example: Bryan and Hartl, 1988; Hartl, 1989). Each red spot corresponds to an excision event, and the size of a red spot is related to the excision time during the development. To quantify the rate of excision in a single individual, 4 classes of mosaic flies (Mos-0, Mos-1, Mos-2 and Mos-3) were defined according to Capy *et al* (1990s); see also table I for a definition of the classe.

Table I. Percentage of mosaic flies (males) in the progeny of test-crosses between wild-type males of isofemale lines and *GB1* females. The F_1 males are classified according to the number of independent excision events (number of red spots on both eyes) as: Mos-0 for *white peach* individuals (no mosaic), Mos-1, 2 and 3 phenotypes for mosaic flies with 1-6 spots, 7-20 spots and > 20 spots respectively (Capy *et al*, 1990).

Population	*phenotype*	*Temperature*		
		17° C	*25° C*	*29° C*
		$N = 22$	$N = 22$	$N = 22$
Agadir	Mos-0	20.23 ± 3.94	24.64 ± 4.11	18.87 ± 2.97
	Mos-1	37.45 ± 4.10	37.68 ± 4.88	29.37 ± 4.26
	Mos-2	24.68 ± 4.14	20.59 ± 4.38	20.59 ± 4.01
	Mos-3	17.64 ± 5.95	17.09 ± 6.12	31.18 ± 7.27
		$N = 30$	$N = 31$	$N = 31$
Bordeaux	Mos-0	66.80 ± 4.61	56.48 ± 4.84	41.87 ± 4.91
	Mos-1	23.70 ± 3.06	37.42 ± 4.09	38.55 ± 4.24
	Mos-2	7.93 ± 2.79	3.29 ± 0.89	10.58 ± 3.05
	Mos-3	1.57 ± 1.08	2.81 ± 2.25	9.00 ± 3.70
		$N = 25$	$N = 22$	$N = 21$
Loua	Mos-0	85.08 ± 2.68	62.41 ± 5.82	50.48 ± 6.78
	Mos-1	14.44 ± 2.63	33.27 ± 5.80	38.76 ± 6.01
	Mos-2	0.28 ± 0.16	2.59 ± 1.23	5.14 ± 1.52
	Mos-3	0.20 ± 0.20	1.73 ± 0.97	5.62 ± 2.37

N = number of isofemale lines.

Estimation of the somatic excision rate

The somatic excision rate, in each isofemale line, was estimated after a test-cross between 5 males of the line tested and 5 females of the *GB1* strain (figure 1). The latter strain of *D simulans*, built by Glenn Bryan (Bryan and Hartl, 1988), contains a single inactive element (the *peach* element) inserted in the *white* gene. This element was introduced in *D simulans* from the *white peach* strain of *D mauritiana*, after an interspecific cross followed by several backcrosses. The *GB1* strain is extremely stable and no revertant has been observed. The somatic excision rate was estimated by the ratio of mosaic males observed in the F_1 of the test-cross over the total number of F_1 males examined, *ie* at least 10 males/line but when possible 50 males/line.

Southern blots

For each isofemale line, DNA of 25–30 individuals was prepared, as described by Junakovic *et al* (1984), completely digested with the restriction enzymes *Bam*HI and *Hin*dIII, which do not cut in the element, and loaded in a single lane of a 0.8% gel agarose. To detect all elements (complete and deleted), filters were then

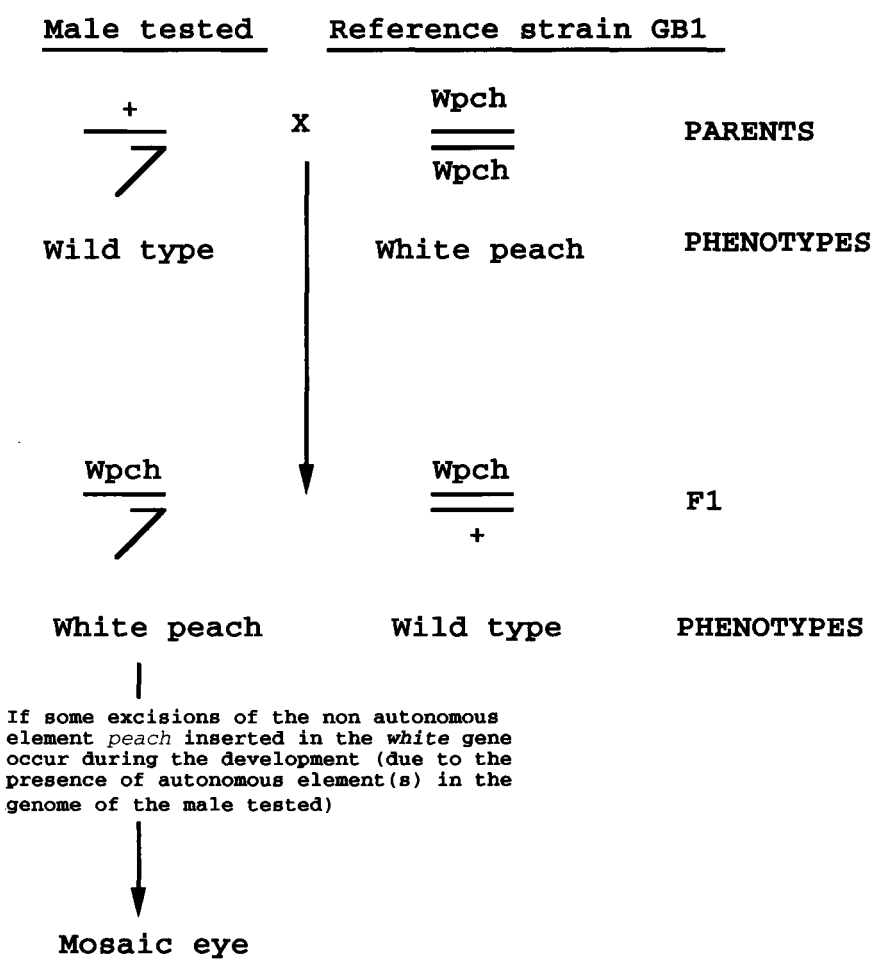

Fig 1. Test-cross used to estimate the somatic excision rate (see text for the details of the cross). The mosaic males in F_1 are classified from Mos-0 to Mos-3 according to the number of independent excisions (number of red spots) that can be observed on both eyes.

hybridized with a mixture of the *Ssp*I-*Xho*I and of the *Xho*II-*Nhe*I fragments of *mariner* (see Maruyama and Hartl, 1991). These 2 fragments cover 1.1 kb of the total element (total length of the element = 1.286 kb). These probes were labelled by nick translation according to Maniatis *et al* (1982). Hybridization and washing procedures were as Junakovic *et al* (1984).

RESULTS

Temperature effect

Table I gives the percentage of mosaic flies (PMF) in each population for the 3 breeding temperatures and statistical comparisons are given in table II. The 3 populations present some different PMF, the average values always being higher in Agadir than in the 2 other populations whatever the breeding temperature. A detailed analysis of table I shows that the PMF belonging to the Mos-3 class is also higher in Agadir than in Bordeaux and Loua where the Mos-0 (no mosaic) individuals are more abundant.

Table II. Analysis of variance of the percentage of mosaic flies (PMF) for the 3 natural populations.

Population	*Source of variation*	*DF*	*Mean square*	F
Agadir	Temperature	2	197	0.85
	Line	21	453	1.95
	Residual	42	232	
Bordeaux	Temperature	2	5158	14.10***
	Line	30	1370	3.75*
	Residual	59	364	
Loua	Temperature	2	9130	27.40***
	Line	24	1515	4.58*
	Residual	41	332	

* $p < 0.05$; *** $p < 0.001$.

The PMF increases with temperature for Bordeaux and Loua but not for Agadir. The differences between the total PMF at 17 and 29°C are statistically significant only for the first 2 populations. Concerning Agadir, the PMF seems to be independent of the temperature. Such a result can also be due to the method used to quantify the amount of independent excisions in each individual. With this method, it is almost impossible to discriminate between individuals having a high level of somatic excision, since all of them are grouped in the Mos-3 class. In other words, it is possible that a temperature effect still existed in the Agadir population but such effect could not be quantified because the basic excision rate, in this population, remained high whatever the breeding temperature.

Table II shows that in Bordeaux and Loua both temperature and isofemale line effects were detected, but not in Agadir. Again, a more detailed analysis, class by class, showed that the temperature effect was higher in population in which the main class at 17°C was the Mos-1, *ie* Loua and Bordeaux. In these populations, the average number of Mos-1 individuals decreases at 25°C and 29°C, while the average number of Mos-2 and Mos-3 individuals increases.

Average number of copies per isofemale line

The average number of copies (ANC) per isofemale line was estimated by counting the number of bands on Southern filters (fig 2). This average number includes both active and inactive copies. A large polymorphism was observed both within and between populations. In each population, it is possible to find some isofemale lines with a high or a small number of copies (see fig 2). For instance, for Agadir, line 21 presents an ANC of 17 elements while a single element was detected in line 12. The same phenomenon can be observed for the 2 other populations but the highest ANCs per line were observed for Agadir. On the other hand, it must be stressed that no line was found to be totally free of *mariner*, and that the average number of copies were under-estimated since co-migration of bands and degradation of high molecular weight bands may occur.

In this analysis 30, 22 and 21 isofemale lines were tested for Bordeaux, Loua and Agadir, respectively, and the ANC per line are 7.9 ± 1.2 for Agadir, 5.2 ± 0.5 for Bordeaux and 4.7 ± 0.6 for Loua. The classification of populations is the same as regards the PMF and the ANC, *ie* Agadir, Bordeaux and Loua, from the highest to the lowest values. Within each population, a Spearman rank correlation test between the PMF and the ANC of the different lines for each breeding temperature, showed only 1 significant correlation. Seven out of 9 coefficients were positive, but not all coefficients were independent since the numbers of *mariner* copies per line were used for the 3 temperatures. Therefore, although some tendencies are suggested, it remains difficult to conclude that a relationship exists between the excision rate and the number of copies in wild populations, and such a result has to be confirmed from a larger set of data.

DISCUSSION AND CONCLUSION

Our results show that in some natural populations of *D simulans*: 1) there is a temperature effect on the somatic excision rate of an inactive copy of the *mariner* transposable element, 2) this temperature effect may vary from one population to another and 3) the between-population variability of the excision rate measured by the PMF could be related to the average number of *mariner* copies per population.

The relationship between the excision rate and the breeding temperature suggests that a promoter acting on the transposase production is sensitive to temperature. This could be an internal promoter of the transposase, included in the transposable element itself, or an external promoter, close to the insertion point of the transposable element. In this respect, the role of the genetic environment seems to be an important component of *mariner* element activity as already demonstrated by the position effects frequently observed (Garza *et al*, 1991; Maruyama *et al*, 1991; Medhora *et al*, 1991).

A comparison between the *mariner* sequence in 5′ of the initiation site and the promoter sequence of several heat shock genes was made (table III). Homology of 57% between a 14-bp sequence in the inverted repeat of the *mariner* transposable element and a putative promoter of *hsp-70* was detected (see: Strand and McDonald, 1985; and references therein). Homologies of 50% were also observed with other

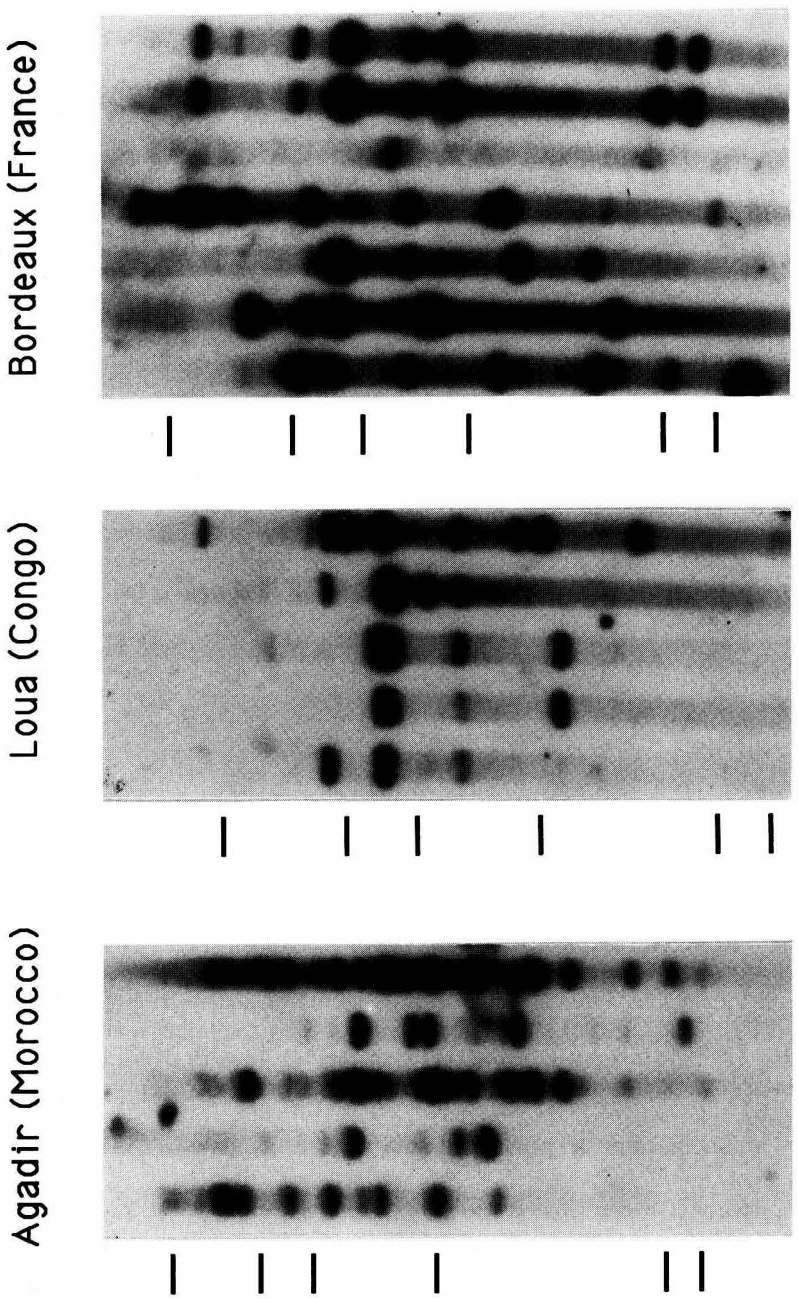

Fig 2. Southern blots of total genomic DNA of Agadir, Loua and Bordeaux isofemale lines. The genomic DNA of ≈ 25 flies were digested by *Hin*dIII and *Bam*HI, and probed simultaneously with pchIV and pchV, 2 *mariner* fragments which cover the total length of the element (see Maruyama and Hartl, 1991).

Table III. Comparison between a 14-bp sequence localized in the 5′ inverted repeat (IR) of the *peach* element and several promoter sequences of *hsp* and of the transposable element *copia*. Consensus sequence is derived from a set of *hsp* promoter sequences given and referenced by Strand and McDonald (1985).

Gene	*Promoter sequence*	*Similarity with* peach *IR (%)*
Consensus	CTgGAAtnTTCtAG	50
hsp-23	CGAGAAGTTTCGTG	50
hsp-27	ATTAAGTTCCGTC	50
hsp-68	CTGGAATGTTCTGA	50
hsp-70	TGCGAATGTTCGCG	57
copia	TTGGAATATACTAT	50
peach	AGGGAATGTCGGTT	

sequences of heat shock promotors and with a 14-bp sequence of the *copia* transposable element (sequence localized in position − 110 bp from the transcriptional start, *ie* in the LTR of the element). For this latter element, a temperature effect on the transcription rate was also described (Strand and McDonald, 1985). In the case of *mariner*, it is thus possible that the thermosensitivity of the transcription rate is an intrinsic property of its 5′ inverted repeat.

Another mechanism which could explain a relationship between the breeding temperature and an excision rate would be a thermal degradation of a product involved in the repression of the element mobility. In *mariner*, several position effects have been described (Maruyama *et al*, 1991), but we do not know whether there is a positive or a negative effect of the genetic environment on the transposase production by autonomous elements. In case of a negative effect, a thermal sensitivity of a product responsible for such a repression should result in an increase of transposase production and in an increase of excision rate. For the moment, data are available on neither the transposition nor regulation mechanisms of the *mariner* element to test this hypothesis.

In the 3 populations investigated, our results suggest that a relationship exists between the average number of copies and the activity level of the *mariner* elements measured by the excision rate. Although the presence of active elements is these populations is confirmed, it is however not possible to estimate the number of active copies in each population and each isofemale line.

The activity of the *mariner* element may vary according to its own sequence and to its genomic position (Maruyama *et al*, 1991; Medhora *et al*, 1991; Capy *et al*, 1992). Therefore, a given excision rate can be due to a single element highly active or to several elements with a low activity. In this latter case, a dosage effect could exist. Such a dosage effect, for the *mariner* element, has already been stressed by Garza *et al* (1991). In the present work, it is likely that the transposable production is higher in Agadir than in Bordeaux and Loua. In other words, it is possible that Bordeaux and Loua were genetically more stable than Agadir at the moment of their sampling.

The variability of the temperature effect observed between the three natural populations raises the following question: does this variability correspond to genetic drift between geographically distant populations or to different local adaptations?

Very few data are available on transposable elements in natural populations originating from different biogeographic areas. For numerous genetical traits, like morphological traits or enzymatic polymorphism, it seems that in *D melanogaster* (a sibling species of *D simulans*), an influence of the average temperature is likely for the occurrence of latitudinal clines (Lemeunier *et al*, 1986; David and Capy, 1988). *D simulans*, on the other hand, generally exhibits a lower geographic differentiation, although regular latitudinal variations have been observed in several cases (Parsons, 1983; Lemeunier *et al*, 1986; Hoffmann and Parsons, 1991). Therefore, such a climatic factor is able to induce genetic variations among natural populations of cosmopolitan species. To detect a variability of temperature effect on excision rate of transposable elements according to the average temperature of the geographic area of natural populations, many more populations should be investigated.

In conclusion, it seems that temperature is one of the environmental factors able to induce the somatic transposition of the *mariner* element in natural populations of *D simulans*. However, populations with high basic excision rate could remain insensitive to this factor.

For the moment, the data available are not sufficient to check this conclusion. But, it must be stressed again that for *Drosophila*, temperature is a factor which shows seasonal and daily variations in several places. Therefore, it is possible that temperature can induce genomic stresses strong enough to stimulate mobilisation and rearrangement of transposable elements. If so, the reasons and the mechanisms of these remain to be investigated.

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