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Behaviour of the transposable elements *copia* and *mdg1* in hybrids between the sibling species *Drosophila melanogaster* and *D. simulans*

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The behaviour of the retrotransposons *copia* and *mdg1* was analysed in hybrids between *Drosophila melanogaster* and *D. simulans*. Females of a highly inbred line of *D. melanogaster* were crossed with *D. simulans* males from three natural populations. The insertion site profiles for the two elements were determined in F_1 hybrid larvae by *in situ* hybridization to polytene chromosomes, and were compared with that of their parents. No somatic transposition events were detected after this genomic stress of interspecific hybridization for the two transposable elements concerned.

Keywords: *Drosophila melanogaster, D. simulans*, interspecific hybrids, transposable elements.

Introduction

Although transposable elements usually move in the germ line at a low rate, mobilization can be observed in intra- and interspecific hybrids. A well documented case is the phenomenom of hybrid dysgenesis in *Drosophila* in which P elements transpose after intraspecific crosses. Indeed the P/M, I/R and hobo hybrid dysgenesis systems in *D. melanogaster* are capable of activating transposable elements, inducing sterility, gonadal atrophy and of increasing the mutation rate in F_1 progeny of intraspecific crosses between males from a natural population and females from a long established laboratory strain. Retrotransposons can also be mobilized after crosses involving laboratory or wild lines and some balancer stocks as observed in Pasyukova *et al.* (1988), Georgiev *et al.* (1990), Pasyukova & Nuzhdin (1993) and Garcia Guerreiro & Biémont (1995).

Genetic instabilities, measured as an increase in mutation rate, were observed in some cases. In maize, for example, the nuclear DNA content of some F_1 hybrids from crosses between different inbred lines was significantly higher than their parental means. This nuclear instability depended on the parental inbred lines used in each cross (Rayburn *et al.*, 1993).

Interspecific hybridization seems also to be associated with genomic instabilities as demonstrated mainly in plants. Price (1988) suggests that some portions of the DNA are unstable in various hybrids of the genus *Microseris* (Asteraceae) in such a way that these hybrids have nuclear DNA contents that differ significantly from the parental midpoint and that these instabilities can fluctuate randomly. Unusual chromosomal rearrangements were also reported in hybrids between two species of *Nicotiana* (Gerstel & Burns, 1966). In *Drosophila*, gonadal atrophy, mutations and elevated rates of chromosomal breakage have also been observed in interspecific crosses between sibling species (Sturtevant, 1939; Naveira & Fontdevila, 1985). In some of these *Drosophila* hybrids, germline transposition seems to occur (Evgen'ev *et al.*, 1982; Labrador & Fontdevila, 1994) at a rate similar to those reported previously in dysgenic lines of *D. melanogaster* (Fontdevila, 1993). The causes of transposition induction in interspecific hybrids are not known but the observation that syndromes characteristic of hybrid dysgenesis are common to both intraspecific and interspecific crosses suggests analogies with this phenomenon.

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Only a few data are available about the transposition rates of interspecific hybrids of *Drosophila*. These data concern the repleta and virilis *Drosophila* groups in which hybrids were checked only for germinal transpositions and the analyses have been carried out many generations after the hybridization event, sometimes 200 generations after (Evgen'ev *et al.*, 1982).

Most of the results mentioned in the literature refer to the germline and no data are available about somatic transposition rates in F_1 interspecific hybrids of *Drosophila*, for which the genomic stress is expected to be very high. Nevertheless, somatically active transposable elements have been identified in *D. melanogaster* (Blackman & Gelbart, 1989; Georgiev *et al.*, 1990; Kim & Belyaeva, 1991a,b), *D. mauritiana* (Hartl, 1989), *Caenorhabditis elegans* (Emmons & Yesner, 1984; Moermann & Waterson, 1989), *Zea mays* (Federoff, 1989), *Antirrhinum majus* (Coen *et al.*, 1989) and mice (Seperack *et al.*, 1988). Moreover, increases of somatic mutations under such stress conditions as high developmental temperatures (Getz & van Schaik, 1991) and a reduction of the lifespan in males with P elements structurally modified by mutagenesis (Woodruff, 1992) have been reported. These phenomena probably result from P element mobilization in dysgenic hybrids.

For retrotransposable elements it is generally accepted that these elements do not undergo transposition during ontogenesis and are stable in somatic cells (Ananiev & Ilyin, 1989; Di Franco *et al.*, 1989). However, the results of Kim & Belyaeva (1991b), where the *gypsy* element was mobilized in somatic cells of male offspring of an individual mutator strain crossed to attached-X females, leave open the possibility that the somatic mobilization of retrotransposons occurs under some conditions.

I have investigated the insertion profiles of two retrotranspons, *copia* and *mdg1*, in interspecific hybrids between the sibling species *D. melanogaster* and *D. simulans*. Hybrids between these two species are usually sterile or inviable (Bock, 1984) but hybrid larvae can be obtained in some cases. I found that the insertion profiles of these F_1 hybrid larvae did not show any mobilization of the two retrotransposons analysed.

Materials and methods

Drosophila *strains*

Line 16 is a highly inbred line of *D. melanogaster* established in 1984 (Biémont & Aouar, 1987) and maintained by brother–sister crosses for about 100 generations and then by mass culture to avoid fertility decrease. The *copia* and *mdg1* insertion profiles showed high stability through many generations. At the time of our experiments *copia* elements were inserted in sites (3F), 12F, 15C, 25A, 26D, (28D), 30D, 42B, 50A, 57C, 67E, 75A, 82E, (90B), 92E, (95DE) and 100B, and *mdg1* elements in sites 3B, 4E, 7B, 11C, 19F, 25A, 35CD, 37A, 39F, 59E, 53C, 52A, 49CD, 42B, 41, 78A, 75C, 85D and 86C (the sites that are not present in all the larvae analysed are shown in parentheses).

The *D. simulans* populations used were recently caught in Valence (France), Madeira island, and Russia. After their arrival in the laboratory different isofemale lines were established and each was maintained by mass culture. These *D. simulans* populations all have a low copy number of *copia* with three fixed sites. At the time of the experiments *copia* elements were inserted at sites 42B, 42C and 82E in the Valence population, 42B, 42C and 82E in the Madeira population and 42B, 42C, 63C and 82E in the Russian population. *mdg1* was not detected in any of these populations.

Crosses

Twenty *D. melanogaster* virgin females a few hours old were placed in vials with 20 *D. simulans* young males. I chose young flies because mating *D. melanogaster* females with *D. simulans* males is easier when flies are a few hours old than when they are 3 or more days old (Pontecorvo, 1943). Crosses were carried out at 20°C because low temperature (18°–22°C) makes them easier (Sturtevant, 1929; Watanabe *et al.*, 1977; Lee, 1978). The pairs were left together for 10 days to guarantee crossing.

Of six populations of *D. simulans* tested, only males from the three populations given above hybridized with females of *D. melanogaster* to give offspring. Moreover, the degree of hybridization observed in the three populations was different: Russia and Madeira showed a higher degree of hybridization than did the Valence population.

DNA probes

I used a fragment of the *mdg1* element (5.6 kb) inserted at the *Hin*dIII site of the PBR322 plasmid (Ilyin *et al.*, 1980; Tchurikov *et al.*, 1980), the probe cDm 5002 containing the *copia* element (5 kb) and a genomic fragment that hybridizes in the 5A region of the X chromosome (Dunsmuir *et al.*, 1980; Levis *et al.*, 1980).

Table 1 Insertion profiles of *copia* and *mdg1* transposable elements in hybrid progeny obtained by crosses of *Drosophila melanogaster* females from the inbred line 16 and *D. simulans* males from a Valence natural population

copia													*mdg1*										
2	3	4				6		8					2	3	4					6		8	
X																							
													3B	3B	3B	3B	3B	3B	3B	3B	3B	3B	3B
12F	12F	12F	12F	12F	12F	12F	12F	12F	12F	12F	12F	12F	4E	4E	4E	4E	4E	4E	4E	4E	4E	4E	4E
15C	15C	15C	15C	15C	15C	15C	15C	15C	15C	15C	15C	15C	7B	7B	7B	7B	7B	7B	7B	7B	7B	7B	7B
19A	19A	19A	19A	19A	19A	19A	19A	19A	19A	19A	19A	19A	11C	11C	11C	11C	11C	11C	11C	11C	11C	11C	11C
													19F	19F	19F	19F	19F	19F	19F	19F	19F	19F	19F
2L																							
25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A
26D	26D	26D	26D	26D	26D	26D	26D	26D	26D	26D	26D	26D	35CD	35CD	35CD	35CD	35CD	35CD	35CD	35CD	35CD	35CD	35CD
28D	28D	28D	28D	28D	28D	28D	28D	28D	28D	28D	28D	28D	37A	37A	37A	37A	37A	37A	37A	37A	37A	37A	37A
30D	30D	30D	30D	30D	30D	30D	30D	30D	30D	30D	30D	30D	39F	39F	39F	39F	39F	39F	39F	39F	39F	39F	39F
2R																							
42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B	42B
42C	42C	42C	42C	42C	42C	42C	42C	42C	42C	42C	42C	42C	44F	44F	44F	44F	44F	44F	44F	44F	44F	44F	44F
44B							44B	44B					49CD	49CD	49CD	49CD	49CD	49CD	49CD	49CD	49CD	49CD	49CD
50A	50A	50A	50A	50A	50A	50A	50A	50A	50A	50A	50A	50A	52A	52A	52A	52A	52A	52A	52A	52A	52A	52A	52A
57C	57C	57C	57C	57C	57C	57C	57C	57C	57C	57C	57C	57C	53C	53C	53C	53C	53C	53C	53C	53C	53C	53C	53C
													59E	59E	59E	59E	59E	59E	59E	59E	59E	59E	59E
3L																							
75A	75A	75A	75A	75A	75A	75A	75A	75A	75A	75A	75A	75A	78A	78A	78A	78A	78A	78A	78A	78A	78A	78A	78A
67E	67E	67E	67E	67E	67E	67E	67E	67E	67E	67E	67E	67E	75C	75C	75C	75C	75C	75C	75C	75C	75C	75C	75C
3R																							
82E	82E	82E	82E	82E	82E	82E	82E	82E	82E	82E	82E	82E	85D	85D	85D	85D	85D	85D	85D	85D	85D	85D	85D
													86C	86C	86C	86C	86C	86C	86C	86C	86C	86C	86C
90B	90B	90B	90B	90B	90B	90B	90B	90B	90B	90B	90B	90B	92A	92A	92A	92A	92A	92A	92A	92A	92A	92A	92A
92E	92E	92E	92E	92E	92E	92E	92E	92E	92E	90E	90E	90E	96F	96F	96F	96F	96F	96F	96F	96F	96F	96F	96F
	95DE		95DE	95DE				95DE		95DE	95DE	95DE											
100B	100B	100B	100B	100B	100B	100B	100B	100B	100B	100B	100B	100B											

Numbers at the top of each column represent the vials from which the larvae came.

In situ *hybridization*

Polytene chromosome squashes from salivary glands of third instar larvae were treated with nick-translated biotinylated DNA probes as described in Biémont (1994). Insertion sites were visualized by a coupled reaction with peroxidase substrate and diaminobenzidine. The insertion pattern of transposable elements of different larvae and four different chromosome spreads on the same slides was analysed under a phase contrast microscope.

Results and discussion

Tables 1–3 give the *copia* and *mdg1* insertion profiles of the hybrid larvae obtained after crosses of *D. simulans* males with inbred *D. melanogaster* females. The *copia* and *mdg1* insertion patterns of the hybrids were the same when different chromosome spreads were compared on the same slide. Moreover, the profile of these elements is exactly the sum of the copy numbers of the two parents, as expected given that the parents were homozygous. No strong evidence of transposition events was detected for either *copia* or *mdg1* in interspecific hybrids when compared with the profiles of their parents. The only exceptions were the sites 44B (Table 1) and 44F (Tables 1–3) for the *copia* and *mdg1* elements, respectively. These sites were absent in the larvae of the inbred line 16 analysed but present in some hybrid progenies. Because these sites were present in independent progenies of the

Table 2 Insertion profiles of *copia* and *mdg1* transposable elements in hybrid progeny obtained by crosses of *Drosophila melanogaster* females from the inbred line 16 and *D. simulans* males from a Madeira natural population

copia			*mdg1*								
1			1						2		
X											
			3B	3B	3B	3B	3B	3B	3B	3B	3B
12F	12F	12F	4E	4E	4E	4E	4E	4E	4E	4E	4E
15C	15C	15C	7B	7B	7B	7B	7B	7B	7B	7B	7B
			11C	11C	11C	11C	11C	11C	11C	11C	11C
			19F	19F	19F	19F	19F	19F	19F	19F	19F
2L											
25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A	25A
26D	26D	26D	35C	35C	35C	35C	35C	35C	35C	35C	35C
28D	28D	28D	37A	37A	37A	37A	37A	37A	37A	37A	37A
30D	30D	30D	39F	39F	39F	39F	39F	39F	39F	39F	39F
2R											
42B	42B	42B	42B	42B	42B	42B		42B	42B	42B	42B
42C	42C	42C	42C	42C	42C	42C	42C	42C			
50A	50A	50A	44F	44F	44F	44F	44F	44F	44F	44F	44F
57C	57C	57C	49CD	49CD	49CD	49CD	49CD	49CD	49CD	49CD	49CD
			52A	52A	52A	52A	52A	52A	52A	52A	52A
			53C	53C	53C	53C	53C	53C	53C	53C	53C
			59E	59E	59E	59E	59E	59E	59E	59E	59E
3L											
67E	67E	67E	75C	75C	75C	75C	75C	75C	75C	75C	75C
75A	75A	75A	78A	78A	78A	78A	78A	78A	78A	78A	78A
3R											
82E	82E	82E	82E					82E	82E		
			85D	85D	85D	85D	85D	85D	85D	85D	85D
90B	90B	90B	86C	86C	86C	86C	86C	86C	86C	86C	86C
92E	92E	92E	92A	92A	92A	92A	92A	92A	92A	92A	92A
100B	100B	100B	96F	96F	96F	96F	96F	96F	96F	96F	96F

Numbers at the top of each column represent the vials from which the larvae came.

Table 3 Insertion profiles of *copia* and *mdg1* transposable elements in hybrid progeny obtained by crosses of *Drosophila melanogaster* females from the inbred line 16 and *D. simulans* males from a Russia natural population

copia				*mdg1*				
1			2	1			2	
X								
				3B	3B	3B	3B	3B
12F	12F	12F	12F	4E	4E	4E	4E	4E
15C	15C	15C	15C	11C	11C	11C	11C	11C
				19F	19F	19F	19F	19F
2L								
25A	25A	25A	25A	25A	25A	25A	25A	25A
26D	26D	26D	26D	35C	35C	35C	35C	35C
28D	28D		28D	37A	37A	37A	37A	37A
30D	30D	30D	30D	39F	39F	39F	39F	39F
2R								
42B	42B	42B	42B	42B	42B	42B	42B	42B
42C	42C	42C	42C	42C	42C		42C	
50A	50A	50A	50A	44F	44F	44F	44F	44F
57C	57C	57C	57C	49CD	49CD	49CD	49CD	49CD
				52A	52A	52A	52A	52A
				53C	53C	53C	53C	53C
				59E	59E	59E	59E	59E
3L								
63C	63C	63C	63C	78A	78A	78A	78A	78A
	67E	67E	67E	75C	75C	75C	75C	75C
75A			75A					
3R								
								82E
82E	82E	82E	82E	85D	85D	85D	85D	85D
90B	90B	90B	90B	86C	86C	86C	86C	86C
92E	92E	92E	92E	92AB	92AB	92AB	92AB	92AB
				96F	96F	96F	96F	96F
100B	100B	100B	100B					

Numbers at the top of each column represent the vials from which the larvae came.

populations analysed, I think that the result arises from heterogeneity in the original inbred line 16, which was not detected in the larvae analysed from the inbred line 16. In fact, the insertion polymorphism of this line was regularly checked and it was found that the transposable element insertion profile through generations showed some polymorphism.

The insertion profiles of the *copia* and *mdg1* transposable elements are thus not perturbed in the F_1 hybrids resulting from crossing *D. melanogaster* females with *D. simulans*. Given that zero transposition was observed, the 95% upper confidence limit can be calculated from the Poisson distribution. If the probability of seeing zero insertion is 5%, the number of new transpositions expected is $-\ln(0.05) = 2.9957$. Thus the upper confidence limit on the rate of transposition is $2.9957/n$, where n is the sample size. I have analysed 343 sites for *copia* and 532 for *mdg1* and for each slide I have compared the insertion profile of four spreads per slide. The total sample sizes screened on average in these experiments are thus 1372 for *copia* and 2128 for *mdg1*. The upper confidence limits are 0.00218 transpositions per element and 0.00140 transpositions per element for *copia* and *mdg1*, respectively.

This result differs from the increased frequency of

dysgenic-like events reported in hybrids between *D. buzzatii* and *D. koepferae* with relatively high frequencies of new insertions in the germline (Naveira & Fontdevila, 1985; Labrador & Fontdevila, 1994), and from contamination of *D. littoralis* by transposable elements from *D. virilis* after repeated backcrosses (Evgen'ev *et al.*, 1982). In the last experiment only one new insertion was detected in hybrids analysed 200 generations after the hybridization event leaving open the possibility of a transposition a long time after hybridization. It is also hard to be sure that the new insertion site was not initially present in the original line.

It is important to note that in my case only somatic transpositions were checked because transpositions in the germline cannot be detected at the first generation of hybrid crosses and more generations would have been necessary to detect them. Unfortunately, F_2 progeny could not be analysed because the F_1 females were sterile.

As well as the germline events mentioned above, somatic ones may occur. The transposable element *Tc1* of *C. elegans* is subject to both strain- and tissue-specific controls and in some varieties of the nematode this element is more active in somatic than in germ cells (Emmons & Yesner, 1984). The P element, that is not normally active in somatic cells, can be active in special conditions of hybrid dysgenesis at 29°C (Getz & van Schaik, 1991). It is known that retrotransposons are actively transcribed in somatic cells and are thus able to transpose *in vivo*. The first evidence of somatic transposition of retrotransposons appeared with the *gypsy* element which transposes in germline and somatic cells of one mutator strain (MS) (Kim & Belyaeva, 1991b). Other transposable elements, including *copia* and *mdg1* analysed here, displayed no changes in insertion sites. These results are in agreement with the absence of mobility of the two transposable elements analysed in my study.

Crow (1984) has pointed out that limiting movement of transposable DNA to the germline prevents lethal effects, including cancer, that could occur if these elements moved in somatic tissue. There is probably a strong selective advantage to elements with repressed transposition in somatic tissues. It is suspected that in normal conditions in nature the somatic activity of transposable elements is very low or genetically suppressed (McDonald, 1990) probably because it reduces the fitness of individuals. In my experiments it is expected that the crosses between different species could have broken down the genetic system that represses somatic transpositions. As no somatic transpositions were observed it may be that these elements have no ability to transpose in somatic cells or that the genetic conditions are not suitable to promote transposition.

The causes capable of activating somatic transpositions remain obscure and more work on the behaviour of transposable elements in somatic cells under stress conditions, such as the interspecific hybridization of other *Drosophila* spp., is thus necessary to understand the factors able to promote somatic transposition.

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