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Transposable elements and genome evolution: the case of *Drosophila simulans*

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Abstract

Drosophila simulans presents a large variation in copy number among various transposable elements (TEs) and among natural populations for a given element. Some elements such as *HMS beagle*, *blood*, *flea*, *tirant*, *coral*, *prygun*, *jockey*, *F*, *nomade* and *mariner* are absent in most populations, except in one or two which have copies on their chromosome arms. This suggests that some TEs are being awakened in *D. simulans* and are in the process of invading the species while it is colonizing the world. The elements *412* and *roo/B104* present a wide insertion polymorphism among *D. simulans* populations, but only the *412* copy number follows a temperature cline. One population (Canberra from Australia) has a very high copy number for the *412* element and for many other TEs as well, indicating that some populations may have lost control of some of their TEs. While the *412* transposition rate is similar in all populations, its transcription level throughout developmental stages varies with populations, depending on copy number. Populations with *412* copy number higher than 10–12 exhibit co-suppression, while the expression in populations with lower numbers depends on the insertion location. All these results suggest genomic invasions by *412* and other TEs during the worldwide spread of the *D. simulans* species.

Introduction

Transposable elements (TEs), which have been found in organisms as various as bacteria, arthropods, plants, and vertebrates (Robertson & Lampe, 1995; Heslop-Harrison et al., 1997; Löwer, Löwer & Kurth, 1996), were thought for a long time to be only parasitic elements. It is now evident that they have played an important role in evolution (McDonald, 1995; Kidwell & Lisch, 1997), and by promoting new genetic variability could still be of major importance for population adaptation. Hence, we need to know their dynamic in natural populations. We have, however, little information concerning the way TEs invade populations and on the mechanisms involved in the first step of the invasion. The best known examples are from *Drosophila melanogaster*, which has been invaded only recently by the *P* (Bonnivard & Higué, 1998) and *hobo* (Bonnivard, Higué & Bazin, 1997; Bonnivard et al., 1999) transposons, and the *I* non-

LTR retrotransposon, all elements involved in hybrid dysgenesis (Kidwell & Lisch, 1997). It has also been suggested that the *F* element, a non-LTR retrotransposon, has recently become transposed throughout the *D. melanogaster* genome (Dawid et al., 1981; Vauray, Bucheton & Péliesson, 1989). These findings imply that these TEs have been mobilized in a local natural population or have been acquired in that population as a result of horizontal transfer. They have then invaded the entire species by gradual diffusion of the flies. The *I* and *P* elements invaded the *D. melanogaster* species only during a 50-year period at the beginning of this century. Such rapid and recent invasions suggest that it should be possible to observe other TE mobilizations in present day local populations. We summarize in the present paper the recent information concerning the dynamics of various TEs in natural populations of *D. melanogaster* and *D. simulans*, focusing attention to the *412* element for which more data are available. We propose that the genome of the species

Table 1. Transposable element insertion site number in two isofemale lines from *D. simulans* natural populations

Populations	Transposable elements													
	1731	297	bel	blood	coral	F	flea	gypsy	HMS	mariner	nomade	prygun	stalker	zam
Amieu (New Caledonia)	1-0	0-0	0-0	1-2	0-0	1-1	2-2	0-0	2-1	0-1	0-0	0-0	0-0	1-1
Canberra (Australia)	2-1	1-1	0-0	0-2	4-2	7-14	1-2	3-3	1-4	6-9	8-7	1-0	0-0	0-0
Cann River (Australia)	2-2	1-1	0-0	2-3	1-1	3-3	1-1	1-1	2-2	0-1	2-2	0-0	1-1	0-0
Eden (Australia)	0-2	1-1	1-0	4-3	3-2	1-1	3-5	0-2	0-2	0-2	5-1	0-0	0-0	0-0
Madagascar	1-1	0-0	1-1	0-5	0-0	0-0	3-2	2-2	10-12	1-3	0-0	0-0	0-0	0-0
Madeira (Portugal)	1-1	2-1	1-1	10-10	1-2	0-0	4-4	2-0	5-2	1-1	1-0	0-0	2-2	0-0
Makindu (Kenya)	1-1	2-2	0-0	1-1	6-3	0-0	0-0	2-4	0-0	0-0	0-0	6-7	0-0	0-0
Moscow (Russia)	3-3	0-1	2-1	1-2	4-5	0-0	1-3	2-3	1-0	1-1	1-0	0-0	1-1	0-0
Noumea (Polynesia)	1-0	1-3	1-0	0-1	3-3	1-1	2-4	2-1	4-4	1-0	1-1	0-0	0-0	2-2
Papette (Polynesia)	0-0	2-2	0-2	4-2	0-0	13-0	3-5	4-3	4-4	0-0	6-5	0-0	0-0	0-0
Reunion Island	0-0	2-0	0-2	0-0	1-4	0-0	2-3	2-0	5-5	3-4	1-0	2-1	0-0	0-0
Valence (France)	0-0	1-1	0-0	4-5	1-1	0-0	6-2	0-0	0-2	0-0	4-1	0-0	0-0	0-0
Zimbabwe (Africa)	2-1	0-0	1-1	1-1	1-1	0-0	15-13	0-1	0-0	1-2	1-1	2-2	1-1	0-0

D. simulans is in the process of being invaded by some TEs, which appeared to have been first mobilized in local populations.

TE copy numbers in natural populations of *D. melanogaster* and *D. simulans*

An analysis of 34 elements in individuals from various natural populations of *D. melanogaster* and *D. simulans* has shown that *D. melanogaster* has higher average chromosomal insertion site numbers per genome than *D. simulans* for most TEs (Vieira et al., 1999). Although the distribution in insertion site number is globally normally distributed in *D. melanogaster*, large variation exists among populations of *D. simulans* for the elements *HMS beagle*, *blood*, *flea*, *tirant*, *coral*, *prygun*, *F*, *nomade* and *mariner*. As seen in Table 1, some of these elements are absent in most populations except one or two which have significantly higher copies. Moreover, within a given population, a line may have 1 or 2 copies of an element whereas the other line may be devoid of the element. Such data suggest that some elements have been mobilized in local populations and are at variance with the classical idea that the fewer copies of most TEs in *D. simulans* in comparison with *D. melanogaster* might reflect some specific evolutionary features of the *D. simulans* genome that have the effect of restraining the number of TE sequences in this species (Kimura & Kidwell, 1994). This latter idea

was supported by the observation that the maximum number of *P* sites in *P*-transformed *D. simulans* lines was much lower than the value found in natural or transformed populations of *D. melanogaster* (Rubin & Spradling, 1982; Daniels et al., 1987; Montchamp-Moreau, 1990), and that the rates of transposition and excision of a *mariner* element from *D. mauritiana* introduced into the germline of *D. melanogaster* are about sixfold greater than the rates in strains of *D. simulans* (Garza et al., 1991). These results suggest that a critical TE-threshold may be a species-dependent characteristic.

Our data favor the alternative, but not exclusive, hypothesis that the genome of *D. simulans* has not yet been invaded by many TEs, except by some of them such as *hobo*, *412* and *roo/B104*, and to a fewer extent, *I*, *doc*, *bari-1* and *helena*, with the elements *gypsy* and *ZAM* (two retroviruses), and *1731* (a LTR-retrotransposon), being equally abundant in both *D. melanogaster* and *D. simulans* (Vieira et al., 1999). In the opposite, *D. melanogaster* was invaded a long time ago by most of the TEs analysed, but only recently by *P* and *I* elements (Bucheton et al., 1984; Anxolabéhère, Kidwell & Periquet, 1988), and the *F* non-LTR retrotransposon, which is mostly restricted to the pericentromeric regions in *D. simulans* (Dawid et al., 1981; Vaury, Bucheton & Péliçon, 1989). We thus propose that TEs in the *D. simulans* genome are being awakened and amplified in some populations, as they were a long time ago in *D. melanogaster*. The main consequence of such a proposal is that the

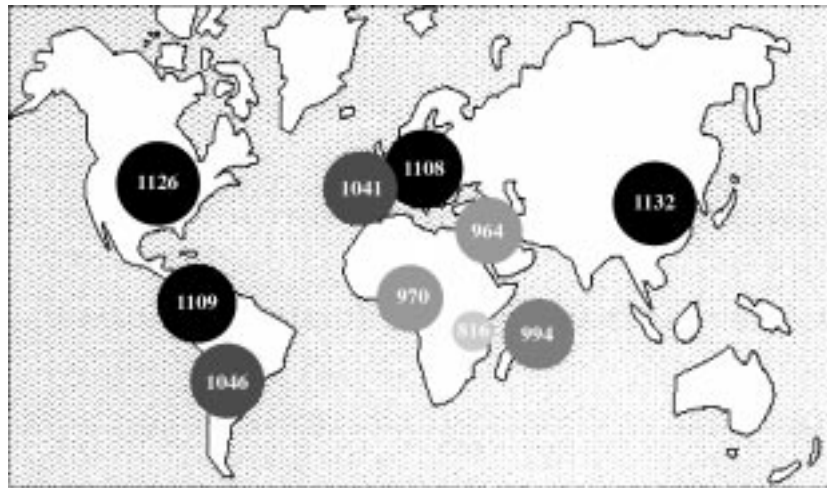


Figure 1. Total number of euchromatic insertions for 30 transposable elements in populations of *Drosophila melanogaster*. The *D. melanogaster* populations considered were from Arabia, Argentina (Virasoro), Bolivia, China (Canton), Congo (Brazzaville), France (St Cyprien), Portugal (Chicharo), Reunion Island, Senegal, and USA (Seattle). Transposons: *bari-1*, *hobo*, *pogo*; LTR retrotransposons: *1731*, *17.6*, *297*, *412*, *bel*, *blood*, *burdock*, *copia*, *coral*, *flea*, *gypsy*, *HMS beagle*, *idefix*, *mdg1*, *mdg3*, *nomade*, *opus*, *prygun*, *roo/B104*, *springer*, *stalker*, *tirant*, *zam*; Non-LTR retrotransposons: *doc*, *F*, *I*, *jockey*.

genome of the *D. simulans* species should gradually be invaded by the TEs mentioned above, with each TE going toward equilibrium for copy number at its own speed. Hence, the apparent critical TE-threshold, which is considered to be a species-dependent characteristic, may only reflect the fact that the populations are far from being at equilibrium for their copy number of most of their TEs because equilibrium state takes a long time to be achieved (Tsitroni, Charles & Biémont, 1999). The observation that elements such as *bari-1* and *hobo* have close copy number in both species means either that *D. simulans* cannot restrain these TEs or more likely that these elements have invaded the *D. simulans* genome long ago before the other TEs. Because *bari-1* and *hobo* are two transposons, it can be argued that *D. simulans* cannot restrain such elements, which differ from the LTR and non-LTR retrotransposons by their transposition mechanism. If this is true, then the argument that *D. simulans* restrains copy number because the maximum number of *P* sites (a transposon) in *P*-transformed *D. simulans* lines was much lower than the value found in natural or transformed populations of *D. melanogaster* can no longer hold. It may be that the populations or lines used in such experiments are more important than the species. The same reasoning as above can be applied to *gypsy* and *ZAM*, two retroviruses, which present 1–2 copies in average in both *D. melanogaster* and *D. simulans*. These elements may be limited in the genome either due to their being deleterious ret-

roviruses or of having invaded the two species only recently. Note that the putative endogenous retroviruses *roo/B104*, *tirant*, and *297* (*roo/B104*, as *gypsy* and *ZAM* has an env-like spliced RNA) have high insertion site number in *D. melanogaster*, suggesting either that this species cannot restrain these retroviruses or that these envelope-containing elements are not true infectious retroviruses.

The 412 retrotransposable element

Among the elements analysed in *D. simulans*, the LTR retrotransposons *412* and *roo/B104*, the non-LTR retrotransposons *I*, *doc*, and *helena*, and the transposon *hobo*, presented a high insertion site copy number with polymorphic insertion localisation (Vieira & Biémont, 1996b; Vieira et al., 1998, 1999). *D. simulans* has, however, fewer copies of these elements, except *hobo*, than *D. melanogaster*. We thus investigated the distribution of the *412* and *roo/B104* elements among natural populations worldwide (Vieira et al., 1998). We showed that the copy number of the *412* element but not *roo/B104* followed a cline with copy number increasing from south to north, and this cline was associated with minimum temperature (Vieira et al., 1998). These data reveal different spatial patterns for the two element families and strongly suggest that some factors in the environment, such as temperature, may interfere with the regulation of copy number. The

presence among the populations tested of one population (Canberra) with a very high copy number of the *412* element, suggests again that a local population may show mobilisation of some of its TEs. In this population the high copy number is not associated with a higher transposition rate (Vieira & Biémont, 1997), suggesting either that the *412* element encountered a temporary burst of transposition followed by a return to normal transposition rate, or that the copy number regulation involves processes independent on that rate. A human-induced migration of alien flies into the Canberra population cannot account for the high copy number because no other population showed such high value; or we have to suppose that mating of flies from different geographic origin can lead to the mobilization of the TEs, in agreement with the higher mutation rate observed in such crosses (Woodruff, Thompson & Lyman, 1979; Thompson & Woodruff, 1980).

The explanation of the difference in copy number of the *412* element among the natural populations could imply either particular sequences in *D. simulans* or specific regulation at the transcription level. We showed that while the canonical structure of the *412* element was conserved between *D. melanogaster* and *D. simulans*, a high structural polymorphism existed among populations with many rearranged copies (Cizeron & Biémont, 1999). *D. simulans* had more rearranged copies than *D. melanogaster*, with some specific copies present in all populations analysed. According to the idea that the rearranged copies should be quickly eliminated by natural selection (Brookfield, 1991), the high number of such copies in the *D. simulans* genome is compatible with recent mobilization and with the fact that selection has not had enough time to strongly reduce the number of these defective copies. Moreover, if one force limiting copy number is to rearrange copies, making them inactive, a functional heterogeneity in a transposable element family may thus have important consequences in limiting the increase in copy number as proposed by Brookfield and Badge (1997). Moreover, full-size and rearranged *412* copies were found both in the euchromatic and heterochromatic regions of the genome (Cizeron & Biémont, 1999). But rearranged copies of various transposable elements are often considered as old genomic components, usually embedded in heterochromatin (Crozatier et al., 1988; Bucheton et al., 1992; Busseau et al., 1994; Vaury et al., 1994), although Sun, Wahlstrom and Karpen (1997) have reported that centromeres may be composed of complete transposable elements. Thus, the fact that the *412* polymorphic

copies appear to be localized in both the heterochromatic and euchromatic genomic regions suggests that the *412* element has been mobilized in the genome of this species only recently, at least more recently than in *D. melanogaster*.

To test the idea that the variation in copy number of the *412* element depends on regulation of transcription, as proposed by Csink and McDonald (1990) for the copia element, we analysed the pattern of expression of the retrotransposable element *412* through developmental stages in various populations of *D. simulans* and *D. melanogaster* (unpublished results). We found that the expression pattern varied greatly with the population considered, and the total amount of transcripts over all developmental stages was lower in *D. melanogaster* than in *D. simulans*. In this latter species the total amount of transcripts increased with the number of copies over the chromosomes until reaching a peak for 11-12 copies and then decreased for higher copy numbers. *D. melanogaster*, which has higher copy number than *D. simulans*, had overall a lower global expression, but showed again variation in *412* expression pattern with populations. These results suggest that in the *D. simulans* populations with low *412* copy number, the expression pattern of this element is mostly dependent upon host cellular regulatory sequences of transcribed cellular genes near which the elements are inserted. In populations with high copy number the overall transcription is, on the contrary, submitted to a global repression. Chromatin-mediated silencing, homology-dependent gene silencing (co-suppression), and other kinds of global repression are proposed as defensive responses of host genomes to TE invasion (Yoder, Walsh & Bestor, 1997; McDonald, 1998; Jensen, Gassama & Heidmann, 1999). Regulation of TE transcription may thus imply host factors, chromatin conformation or internal cis-acting elements (Flavell et al., 1980; Scherer et al., 1981; Parkhurst & Corces, 1987; Cavarec & Heidmann, 1993). The *D. simulans* Canberra population is a special case of interest because it has a *412* copy number much higher than any other *D. simulans* populations (Vieira & Biémont, 1996a), and its high *412* expression seems not to be submitted to the global regulation (unpublished result). This population has either encompassed the normal cellular regulation existing for the *412* element, or it has gained new copies only recently as a result of a recent mobilization of the element (Vieira & Biémont, 1996a). Mobilization within local populations may have resulted from a horizontal transfer from another species,

or from a specific mobilization of inactive or deleted copies already present in the genome. Recombination between homologous elements, even with those in silent chromatin (Ke & Voytas, 1999), and stress induction may all be responsible for the initial steps of TE mobilization and genome invasion. Indeed, recombination and rearrangements between ancient inactive sequences are proposed for the 297 sequence (Martin, Wiernasz & Schedl, 1983) and the *I* elements (Bucheton et al., 1992; Dimitri, 1997). This is compatible with the observation of events in which one element is suddenly mobilized and invades the chromosome arms as reported for elements as diverse as *copia*, *gypsy*, *P* and *doc* in laboratory lines (Biémont, 1992, 1994) and *mdg3* and *412* in natural populations (Biémont et al., 1997; Vieira & Biémont, 1996a). The genome may thus either react to this invasion by producing rearranged copies (Brookfield, 1991), maintain a high copy number, or even keep on accumulating copies if the regulatory pathway of the copy number is overcome. The presence of particular rearranged sequences in all populations of *D. simulans* could thus reflect the reaction of the genome to this invasion at the first steps of this relatively recent event.

Invasion of the genome by TEs follows the species colonisation

The possibility of genome invasion by TEs during the worldwide spread of a species is a challenged idea that is particularly important because recent studies have shown that populations that colonize novel environments can evolve very rapidly in response to natural selection (Orr & Smith, 1998). The idea that TEs can contribute to this adaptation by creating new variability because of their mobilization by the novel environmental conditions is extremely appealing. As seen in the figure, the total amount of TEs determined in various populations of *D. melanogaster* increases from Africa to the other parts of the world. This is compatible with a worldwide colonization by *D. melanogaster* from Africa followed by mobilization of TEs under specific environments in some populations and intense fly migration, the result of which could be a decreased level of activity (Brookfield, 1996; Russel & Woodruff, 1999).

We should then focus our attention on natural populations of species that are in the process of invading new habitats, or living in novel stressful conditions, such as *D. simulans* (Lachaise et al., 1988; Hale &

Singh, 1991) which seems much more variable and may possess greater population substructuring than what we thought (Irvin et al., 1998; Labate, Biermann & Eanes, 1999; Hamblin & Veuille, 1999) with history of founder effects and possible admixture in recently established populations (Hamblin & Veuille, 1999); *D. malerkotliana*, which is spreading rapidly in the far East and tropical Africa (David & Tsacas, 1981); *D. buzzatii*, which has colonized the Iberian peninsula (Labrador, Seleme & Fontdevila, 1998); *Chymomyza amoena*, which has been recently introduced into Europe (Maca & Bächli, 1994; Withers & Allemand, 1998); and any other invading species known for their susceptibility to the environment (see Orr & Smith, 1998, for a review; Duvernell & Turner, 1999) and global change (Duke & Mooney, 1999). We thus need experiments on the sensitivity of TEs to environmental conditions because such a question is central for assessing their contribution to the adaptive capacities of natural populations and speciation.

Induction of TE transpositions by environmental stresses has been demonstrated in only a few cases, in cultured cells and by wounding and abiotic stress in plants (Hirochika et al., 1996; Mhiri et al., 1997), in heated *Saccharomyces cerevisiae* and *Candida albicans* (see Arnault & Dufournel, 1994, for a review), and in *Escherichia coli* after irradiation with UV light (Eichenbaum & Livneh, 1998). It was recently reported that exposure to UV-B of maize sperm at ozone depletion activated immobile Mutator transposons (Walbot, 1998). Since inactive retrotransposons constitute about half the maize genome, mobilization of even a small proportion of these TEs is enough to induce new genetic variation that could be used for adaptation. Some interpretations in *Drosophila* favor the mobilization of retrotransposon elements after heat shock, while other results show no effect of similar stresses (Arnault, Løevenbruck & Biémont, 1997), although heat shock clearly amplifies the amount of transcripts of elements like *copia* (Walbot, 1998). Indirect relationships between environmental factors and mobilization of TEs in *Drosophila* have been reported. For example, the somatic excision rate of the *mariner* transposon increases with the latitude of origin of *D. simulans* populations (Giraud & Capy, 1996) and is related to temperature (Chakrani, Capy & David, 1993). The *412* retrotransposon follows a temperature cline in natural populations of *D. simulans* as reported above (Vieira et al., 1998). Trans-acting regulatory factors that could depend on environmental conditions may regulate TE transposition and excision

rates, but there may also be an indirect effect due to host genes (Bhadra, Pal-Bhadra & Birchler, 1997), whose frequency varies with environmental conditions (Costa et al., 1992; Oakeshott et al., 1992). Migrations and the colonisation of new habitat may thus favor the confrontation between populations which did not meet previously, thus favoring exchange of TEs, as was proposed for the *P* element (Good et al., 1989) and the two species *Drosophila melanogaster* and *D. willistoni* (Daniels et al., 1990). Hybrids between species can even undergo specific amplification and activation of TEs, as in the hybrids of two species of Australian wallaby (*Macropus eugenii* and *Wallabia bicolor*), in which endogenous retroviral elements are amplified many times (O'Neill, O'Neill & Graves, 1998). Whether mobilisation of transposable elements in hybrids is a general process warrants further study, especially because transpositions in interspecific hybrids of *Drosophila* (Evgen'ev et al., 1982; Labrador et al., 1999) have been reported, while the mutation rate did not increase (Coynes, 1989). However, the mutation rate increased in crosses between geographically separated strains (Thompson & Woodruff, 1980).

Conclusion

It is as yet unclear how the new genetic variability resulting from TE mobilization is adaptive. The only experiment supporting this idea is the observation of additional selection response in *Drosophila* lines started from dysgenic crosses known to mobilize *P* elements (Pignatelli & Mackay, 1989). More knowledge on the ecology of *Drosophila* is thus necessary, but the possibility of genome invasion by TEs during the worldwide spread of a species is a challenged idea that warrants examination. Moreover, whether or not such a genomic invasion, which may follow the colonisation process of a species or the increase in connectivity between previously isolated communities, contributes to the C-value paradox of genomes (The DNA amount per genome varies among and even within species. Pagel & Johnstone, 1992; Sherwood & Patton, 1982; Uozu et al., 1997) remains to be determined. Researches should then include the integrated forms of retroviruses whose amount could increase in human societies as a result of increased connectivity between communities through transportation.

Understanding the mechanisms underlying the relationship between dramatic differences in TE copy

number of different species and among natural populations and their environmental conditions is central to understanding the population biology of TEs, and for assessing their contribution to the adaptive capacities of natural populations and speciation. The initially selfish genes will surely appear more and more as 'symbionts' that have played a major role in evolution and that may still provide genomic flexibility and variability for population adaptation.

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