Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Genetics & Development

Transposable elements: all mobile, all different, some stress responsive, some adaptive?

Sophie Lanciano and Marie Mirouze

Transposable elements (TEs) were first identified through the polymorphisms they induced in plants and animals. Genomic studies have later revealed that TEs were highly abundant in eukaryotic genomes. Recently, more precise single individual genomic analyses have unravelled the huge diversity of TE insertions in many plant and animal species. In most cases the stress conditions behind this diversity are not known and neither is the adaptive capacity of these natural TE-induced variants. Here, we review some of the most recent examples of TE-related impacts on gene expression at the locus or the genome level and discuss the rich diversity of the TE repertoire and its potential role in adaptive evolution.

Address
IRD, DIADE, University of Perpignan, Laboratory of Plant Genome and Development, Perpignan, France

Corresponding author:

Current Opinion in Genetics & Development 2018, **49**:106–114

This review comes from a themed issue on **Genome architecture and expression**

Edited by **Kathleen Burns** and **Damon Lisch**

https://doi.org/doi:10.1016/j.gde.2018.04.002

Introduction

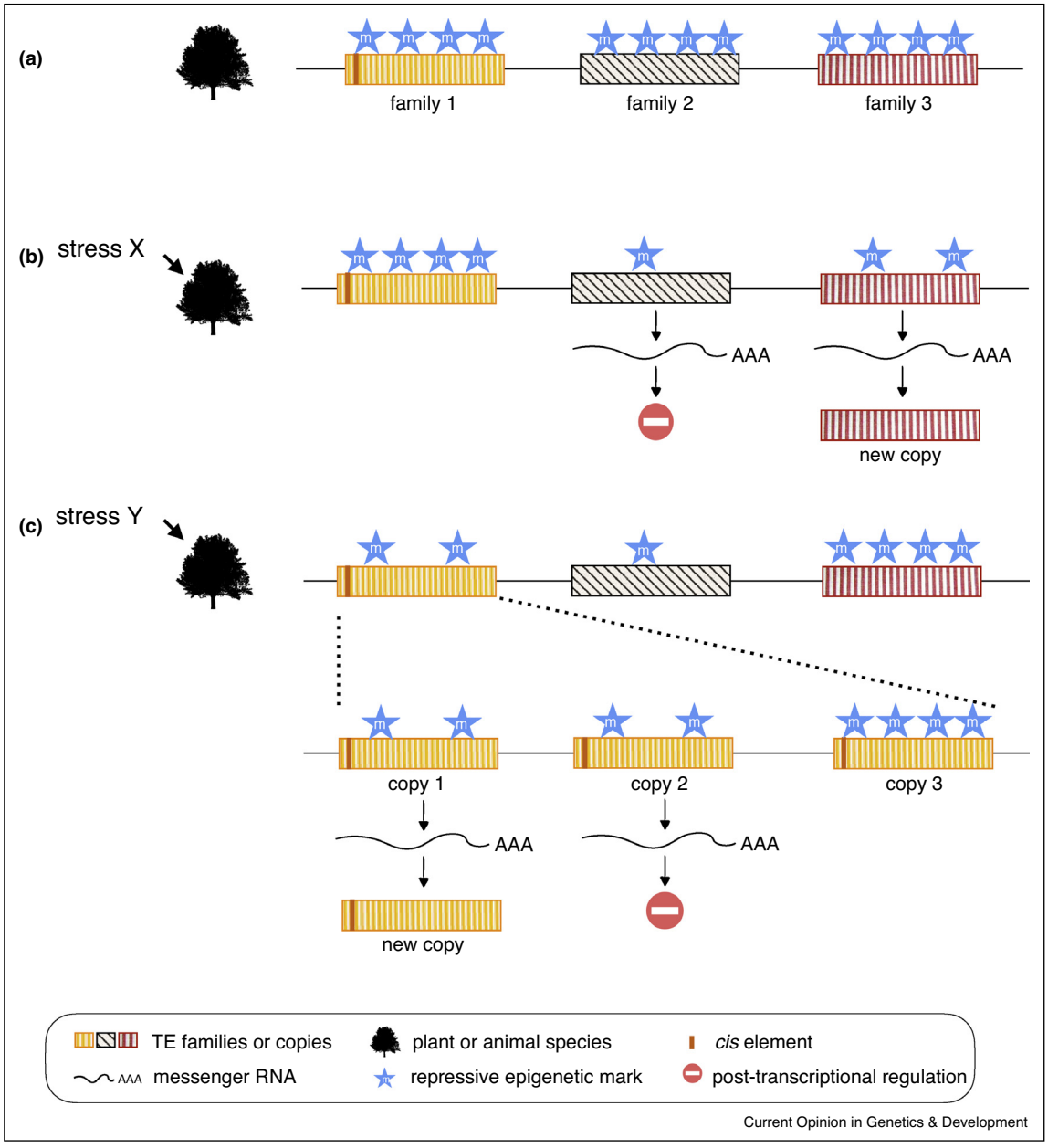
Transposable elements (TEs) are abundant in plant and animal genomes, and their role in genome evolution has been completely revisited in the last decade. Originally viewed as parasitic and/or mutagenic elements (although McClintock [1] and Britten and Davidson [2] had already envisioned in the 1950s their role as controlling elements), they are now considered as drivers in evolution and are the focus of numerous genomic studies. To better understand this paradigm shift, one should first acknowledge the fact that genomic studies have revealed the abundance and ubiquity of TEs. Their activation in response to stress was already noticed in the 1980s when the first retroelements have attracted the attention of scientists [3,4]. The presence of *cis* regulatory elements in their promoters have been intriguing suggesting that, far from junk DNA, TEs could also be involved in complex regulatory processes.

TEs are very diverse and differ in their relative representation in eukaryotic genomes as well as in their mechanisms of regulation and of activation (Figure 1). TEs comprise DNA transposons that move by a cut and paste mechanism and retrotransposons, that move by copy and paste, and these two classes are themselves divided into subclasses, each species containing a specific number of families representing the subclasses. The subclass of long terminal repeat (LTR) retrotransposons is predominant in plant genomes, while non-LTR retrotransposons make up the majority of animal genomes. Non-LTR retrotransposons can nevertheless be abundant in some plant genomes such as that of grapevine and the recently sequenced peanut genome [5], where they represent 10% of the genome. The origin of these species-specific differences is not understood.

TEs are silenced by epigenetic mechanisms, which explains why both the epigenomic landscape and the TE landscape vary between species [6]. Epigenetic regulations are also specific not only to subclasses but also to some TE families. In maize, for example, only some TE families are upregulated in RNA directed DNA Methylation mutants (RdDM, one of the silencing mechanisms controlling TE activity in plants) [7•]. Within these families some loci only can be overexpressed. In human cell lines, different subsets of the non-LTR LINE1 (L1) retrotransposon are active in different cell types [8•]. Epigenetic control might also depend on the age of the TE. Young TEs or intact full length ones seem to be under specific control as exemplified by the RdDM-controlled elements in maize and *Arabidopsis* [7•,9] or the young intronic L1 controlled by a newly identified silencing complex in human cell lines (HUB/MORC2) [10•]. In *Drosophila* hybrids, some TE families are upregulated while others are down regulated, suggesting a complex regulation that may depend on the TE family [11].

Recently, additional posttranscriptional controls such as the one exerted by small RNAs derived from tRNAs revealed in mouse and in *Arabidopsis* [12,13] or the alternative splicing shown in *Drosophila* [14] highlight the complexity of TE control. These examples further reinforce the idea that the transcription of TE families is far from reflecting their transpositional activity. While some geneticists tend to analyze TEs as a whole, it should

Figure 1



The stress response behaviour of TEs is family and copy dependent. **(a)** Example of three TE families repressed in normal conditions by epigenetic marks (e.g. DNA methylation). **(b)** A stress treatment can lead to TE derepression with some families generating new copies (family3) while others are still under posttranscriptional control (family2). **(c)** Here a different stress can lead to the activation of a distinct family (family1) and within this family of only some copies (copy1).

be emphasized that various stress or developmental stages can impact some copies of a particular family, specifically depending on their chromatin environment (Figure 2). The activity of some TEs thus appears to be the result of both a relaxation of the epigenetic control and the recruitment of specific regulatory factors binding to the promoter of the element [15,16,17•].

TEs as responsive elements to environmental stress

TE activation and transposition in response to stress have been dissected in great detail in excellent reviews [18–20]. As transcriptional units, TEs possess their own regulatory sequences that have likely evolved to contribute to their own fitness in their host genome. Interestingly,