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Current Opinion in Plant Biology

Transposons: a blessing curse

Manu J Dubin[1], Ortrun Mittelsten Scheid[2] and Claude Becker[2]

The genomes of most plant species are dominated by transposable elements (TEs). Once considered as 'junk DNA', TEs are now known to have a major role in driving genome evolution. Over the last decade, it has become apparent that some stress conditions and other environmental stimuli can drive bursts of activity of certain TE families and consequently new TE insertions. These can give rise to altered gene expression patterns and phenotypes, with new TE insertions sometimes causing flanking genes to become transcriptionally responsive to the same stress conditions that activated the TE in the first place. Such connections between TE-mediated increases in diversity and an accelerated rate of genome evolution provide powerful mechanisms for plants to adapt more rapidly to new environmental conditions. This review will focus on environmentally induced transposition, the mechanisms by which it alters gene expression, and the consequences for plant genome evolution and breeding.

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Introduction

Transposable elements (TEs) account for the largest fraction of historically called 'junk DNA', that is, DNA stretches without an obvious protein-coding or regulatory functional relevance for the organism. As their name suggests, TEs are mobile within the genome. While type I TEs (retrotransposons) generate an RNA intermediate for a 'copy-and-paste' strategy; type II TEs (DNA transposons) move as DNA via a 'cut-and-paste' mechanism [1]. Both types are sub-divided into classes and clades, based on sequence homology and on whether or not the TEs encode their own transposition machinery. The most abundant TE classes in plant genomes are long terminal repeat retrotransposons (LTRs) and miniature inverted-repeat TEs (MITEs). Although numerous studies on TEs have been conducted in the model plant *Arabidopsis thaliana*, this species is an outlier regarding TE content: TEs make up only 10% of the *A. thaliana* genome, while they account for 85% in maize [2,3] and for 20–40% in rice, depending on species and cultivar [4•]. These species differ not only in absolute TE content, but also in the proportion of TE classes: while type I TEs (LTRs in particular) are the most abundant type in *A. thaliana* and maize [2,3], rice has four times more DNA transposons than retrotransposons (recently reviewed in [5]). This indicates a long and divergent history of TE expansion during plant evolution, with the current situation reflecting a balance between the TEs amplification strategy and the host's defense against resource-requiring genetic parasites.

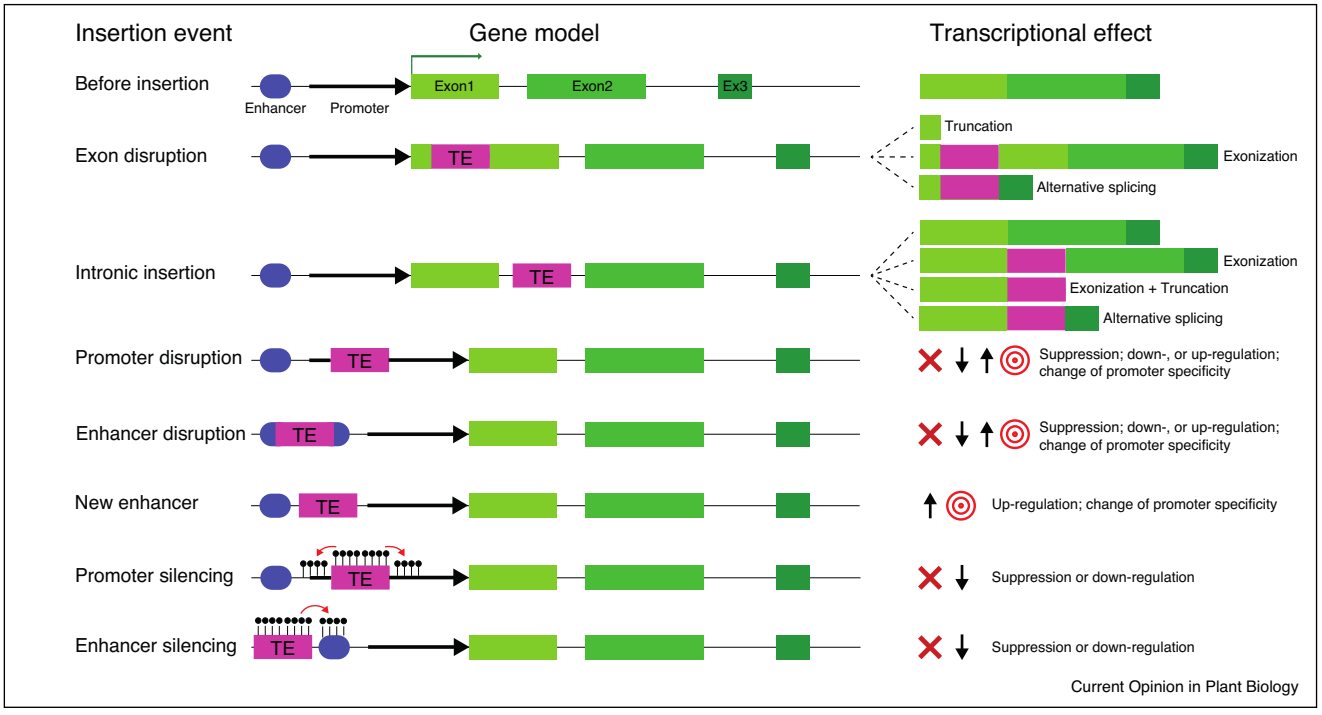
Plants have evolved intricate regulatory machineries to subdue TE mobility and to prevent transposition (recent reviews in [6–8]). Nonetheless, plant genomes carry signatures of massive TE bursts as well as of constant low-frequency transposition [9,10], and it has been postulated that some of these events can act as drivers of genome evolution, expansion, and plasticity [11,12]. Moreover, there is increasing evidence that TEs also play a key role in regulating gene expression. Two possible components of this evolutionary role are reviewed in the following.

Consequences of TE insertions for adjacent genes

The regulation of TE activity and the consequences for the host genome do not only depend on the class of the element but to a large extent also on the site of its insertion. The context-dependent TE regulation is reviewed in detail in [13••]. The accumulation of TEs in gene-poor heterochromatin like pericentromeric regions may be the result of efficient selection against active elements, but many TEs, particularly non-autonomous DNA transposons, are frequent near (<2 kb upstream or downstream) or within genes. Such insertions in protein-coding genes can result in altered expression or modified transcriptional responsiveness of that gene in different ways (Figure 1).

Insertion of a TE into the coding sequence of a gene can disrupt gene function, particularly if located within an exon. This generally results in complete loss-of-function mutations or drastic changes of the encoded protein. Intronic TEs can also have similar effects, for example by altering splicing patterns [14••,15], but may sometimes be spliced out correctly, or alter the ORF marginally.

Figure 1



Effects of TE insertions on gene expression. Consequences of TE transpositions into gene-coding regions depend on the exact location of the insertion and the configuration of the genomic locus. Exonic insertions most frequently lead to truncated or aberrant transcripts; in case of a matching open reading frame (ORF) in the TE sequence, it can result in exonization and the formation of an alternative translatable allele. TEs in introns can have a variety of effects: they can be spliced out, leading to an unaltered transcript, or give rise to new isoforms through exonization, truncation, alternative splicing, or a combination thereof. Outside the transcribed region, TE insertions can disrupt enhancers or regulatory promoter elements, either reducing or potentiating transcription. Spreading of TE-derived epigenetic marks such as DNA methylation (indicated by black pins) into the promoter region usually leads to transcriptional silencing.

Insertion of the TE outside the coding region can interfere with promoter functionality, either by disrupting cis-regulatory regions or transcription start sites, both of which reduce or abolish transcription, or by providing a TE-contained promoter element that boosts gene transcription (see [12,16] for recent reviews of the effects of TEs on gene expression in plants and animals, respectively). Tightly linked is the second mode by which TE insertion in proximity to a gene can influence the expression: if the TEs becomes epigenetically silenced, for example, by RNA-directed DNA methylation (RdDM, reviewed in [17]), their silenced chromatin state can spread to the promoter of neighbouring genes [13••] and suppress their expression.

Examples of functionally relevant TEs are known in tomato [18], melon [19], and orange trees [20], but most prominently in the TE-rich crops rice and maize. This is not surprising as two thirds of maize genes and up to 85% of rice genes have a TE in close proximity (<1 kb) [3,5]. In maize, TEs were found to be associated with major traits such as flowering time [21]; others showed a signature of selection during domestication [22,23] and adaptation to temperate zones [24••]. In this last study, genome-wide association (GWA) mapping in maize inbred lines from temperate and tropical/subtropical cultivars identified an association of a 82-bp long MITE in the promoter of the NAC-type transcription factor *ZmNAC111* with drought tolerance [24••]. The presence of the MITE correlated with lower *ZmNAC111* expression, most likely via RdDM-mediated transcriptional suppression, and higher sensitivity to drought. In rice, phosphate starvation leads to methylation changes preferentially in TEs located close to genes strongly up-regulated under these conditions [25•]. However, methylation changes occurred *after* the transcriptional changes and might thus be a consequence rather than the cause of the shift in expression.

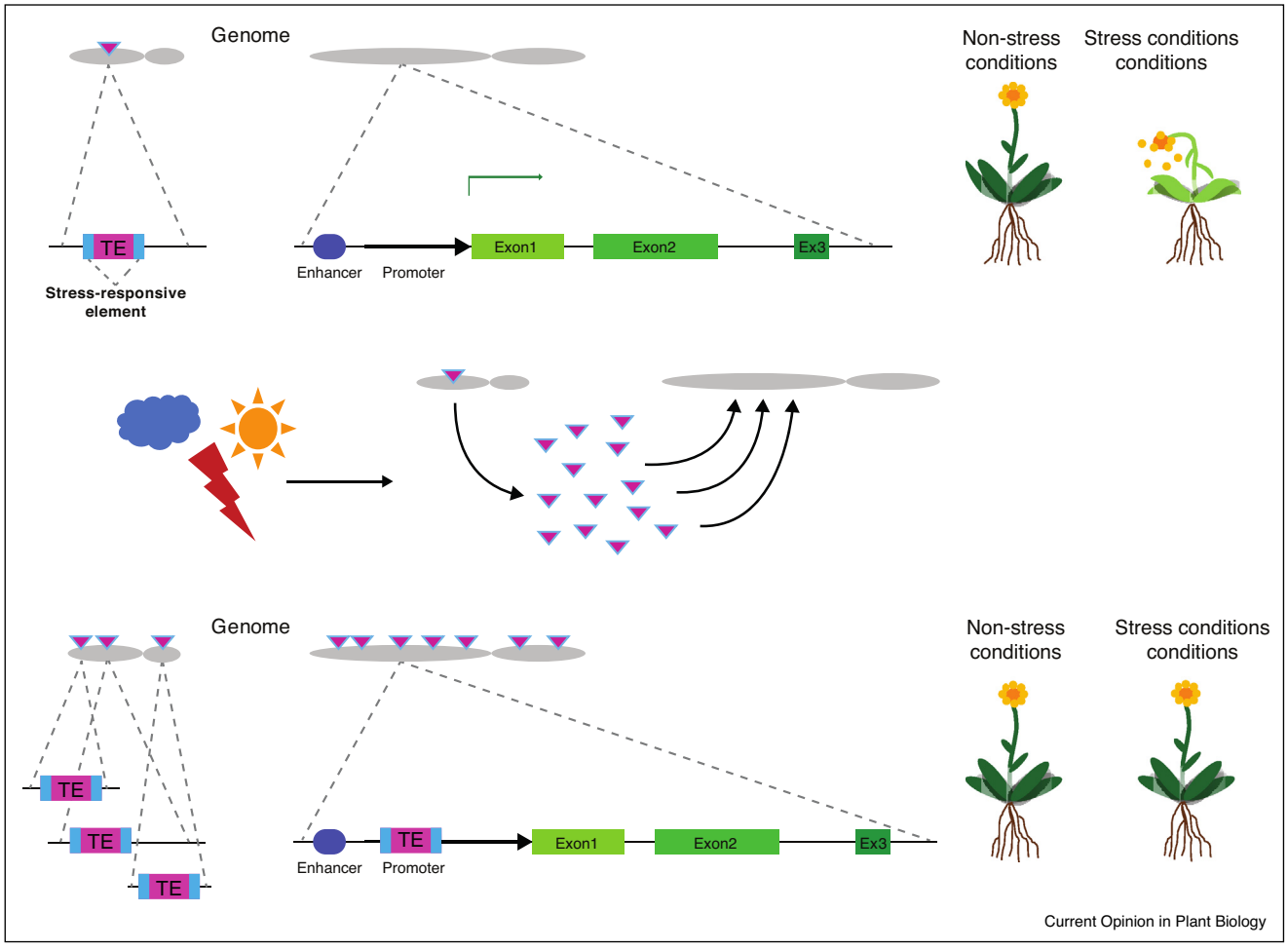
It should be noted that TE-mediated gene regulation is not restricted to TEs located in promoter regions. A remarkable study of somaclonal variation in oil palm revealed that spontaneous loss of DNA methylation at an intronic TE caused aberrant splicing of the homeotic gene *DEFICIENS* transcript, resulting in mantled and thus agronomically useless fruits [14••]. Even when located downstream of a protein-coding sequence, TEs can regulate gene expression: in *A. thaliana*, exposure to

hyperosmotic stress resulted in loss of DNA methylation at a TE downstream of *CARBON NITROGEN INSENSITIVE 1* (*CNI1*) [26•], in turn leading to the expression of an antisense long non-coding RNA (lncRNA) that is likely responsible for the down-regulation of the *CNI1* sense transcript. A more general analysis of long intergenic non-coding RNAs (lincRNAs) in *A. thaliana*, maize, and rice revealed a common pattern of stress-induced lincRNAs coinciding with TEs. Thereby, new TE insertions might enlarge the reservoir of additional and stress-responsive regulatory transcripts with direct influence on the expression level of host genes [27].

Stress-induced TE mobilisation and consequences for genome plasticity

The examples mentioned above demonstrate that the regulatory effect of TE insertions on adjacent genes are especially evident under challenging conditions. This is plausible as some TE families contain stress-responsive elements (SREs) in their own promoters and are themselves responsive to external triggers such as biotic and abiotic stress. Stress-induced TE transcription and in some cases transposition have been observed under different stress conditions and for different classes of TEs [28,29]. SREs are most frequent in some LTR families but also occur in at least one family of MITEs [30]. Upon transposition, these TE-contained SREs can act as new cis-regulatory elements and confer stress-responsiveness to nearby protein-coding genes, thus modifying their functional spectrum (Figure 2). For example, the copia-like retrotransposon *ONSEN* of *A. thaliana* responds to heat stress and can confer heat-responsiveness to genes that are near the new insertion sites [31,32]. Similarly, *mPing*, a MITE DNA transposon in rice confers its own

Figure 2



Abiotic stress conditions induce transposition and/or regulate genes close to residing transposons. Environmental stress induces transcriptional activation of a TE containing a stress-responsive element (light-blue borders) already present in the genome. Such burst of TE expression and amplification of extrachromosomal DNA result occasionally in new insertions at different genomic locations. If inserted within the promoter of a protein-coding gene, the stress-responsiveness of the TE was maintained and the gene product is beneficial for stress tolerance, this combination increases resistance to the stress that initiated the TE burst in the past.

responsiveness to different abiotic stresses to other genes when inserting in their proximity [33]. Stress-inducible TE families seem to preferentially locate close to protein-coding genes. Whether this reflects some selectivity during insertion, or positive selection of the new regulatory potential is difficult to disentangle. TEs containing heat-response elements (HREs) are more highly conserved across members of the Brassicaceae than TEs lacking HREs, suggesting they may be under positive selection [34]. In the most comprehensive study to date on the role of TEs in stress-inducible gene regulation, out of 576 TE families, 20 were found enriched near genes up-regulated by abiotic stress (heat, cold, salt stress or UV), while 3 TE families were enriched near down-regulated genes [35••]. Most importantly, a comparison of TE insertions among three different cultivars revealed that stress-responsiveness strongly depends on the presence of the TE, thus showing that TE polymorphisms can underlie allelic variation in stress responsiveness.

The idea that genetic diversity generated by TEs might facilitate adaptation to stressful conditions (Figure 3), first presented by [11], has been experimentally validated for many cases and is comprehensively reviewed [36••]. Under natural conditions, such adaptations take generations to manifest themselves and to get fixed in a population where the new trait is beneficial. However, these events are also of interest for plant breeding, for example mPing-dependent stress-responsiveness in rice cultivars [30]. Moreover, accelerating and amplifying such adaptive potential seems possible: coupling heat stress exposure with the combined application of a DNA demethylating agent and a Polymerase II inhibitor boosted the mobilization of the heat-responsive *ONSEN* TE in Arabidopsis, generating progeny with high variation regarding phenotypic and stress-responsiveness [37••]. If this approach can be transferred to crop species, it might enable a semi-directional mutagenesis for accelerated plant breeding. It is important to note that stress-induced effects of TEs on gene expression have only been observed for a minority of TE families to date, and examples of stress-induced TE mobility are even rarer. As this field is receiving increasing attention, it will be interesting to see how widespread this phenomenon is.

Impact of TE activity over evolutionary time

The sometimes quite different TE load and distribution between closely related species in different habitats offer great opportunities to learn about the role of TEs for stress resistance over evolutionary time scales. Differences in total TE content and relative abundance of different TE families are responsible for most of the genomic variation between different Brassicaceae [38–40]. Mating system shifts from outcrossing to selfing are unlikely to be responsible: although selfing species generally have fewer TEs and less new TE insertions compared to outcrossers, they do not differ in abundance of particular TE families [41–43]. Large differences in abundance of Gypsy and Copia TEs are also observed among Asteraceae and in particular at the base of the Heliantheae (sunflower), where they are thought to play a role in speciation and are correlated with annual versus perennial life cycles [44,45].

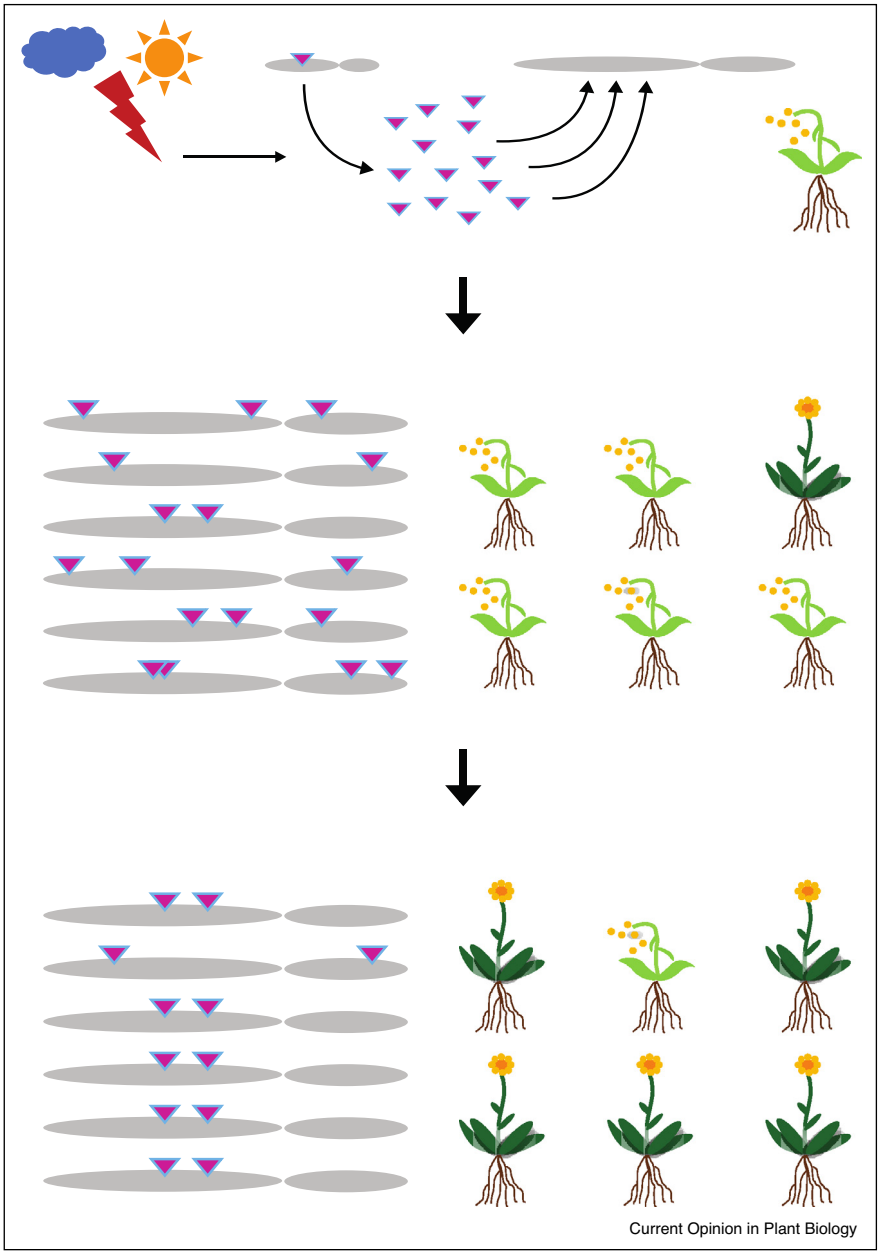
Recent studies have identified over 23 000 *de novo* TE gains and losses within a population of natural *A. thaliana* accessions [46••,47••]. New TE insertions generally occurred at low allele frequencies within the population, suggesting that the majority of events had been deleterious. However, they were overrepresented at some loci, including Nucleotide-binding domain Leucine-rich Repeat (NLR) defense genes, where in some cases they seem to have been advantageous [47••]. Many of the new transposon insertions were in linkage disequilibrium with neighbouring SNPs and thus represent an additional source of genetic diversity not picked up using SNP-based markers [46••]. Interestingly, accessions originating from geographic regions with more variable temperatures also had more insertions of the heat-activated *ONSEN*, including some in the first intron of Flowering Locus C (FLC), a key flowering time regulator. These insertions appear to confer an early flowering phenotype, suggesting that activation of *ONSEN* by warming temperatures may have played a role in the emergence of the rapid cycling in some *A. thaliana* accessions after the last glaciation [47••].

This principle might be paralleled in man-made evolution: compared to their closest wild relatives, domesticated rice cultivars have a striking reduction in the number of TEs located within genes, especially of those in exons. Domestication of rice is also correlated with the gain or loss of TEs at loci involved in flowering time and photosynthetic efficiency [22,23], as well as major domestication-associated loci such as *Grain incomplete filling 1* and *Black hull 4* [4•]. Another example is maize where breeding efforts to adapt ancestral tropical maize varieties to temperate climate zones has resulted in some TE insertions shifting from low allele frequency in the tropical ancestors to medium to high TE allele frequencies in the cold-tolerant lines. Some of these TEs show signs of selection and some are close to loci involved in flowering time and photoperiod response [48•].

Conclusions and outlook

It is now clear that TE-derived DNA sequences are not mere 'junk DNA' but play a fundamental role in regulating gene expression and are an important source of genetic variation in plants. This is highlighted by the massive changes in TE abundance and diversity that occurred during domestication [4•] and as a result of breeding efforts [35••,48•]. Stress-activated TEs can confer new transcriptional responses to the genes flanking their insertion sites. In addition to spontaneously

Figure 3



Transposon-based evolution of stress resistance. Stress-induced new insertions of a transposon create many deleterious genotypes, while those with TE-linked enhanced stress resistance are enriched by natural selection or breeding over time.

occurring random mutations, this provides an additional source of variation on which selection can act to quickly evolve phenotypes adapted to the stress. The ability to artificially boost TE activity provides an extra source of variation for breeding, which is likely to be of increasing importance in the future.

A substantial fraction of recent studies has focused on a few temperature-induced TE families. It is likely, however, that many other environmental conditions or even biotic interactions can induce additional TE families, and this needs to be explored in future work. Research with *A. thaliana* can now be complemented by investigating other plants with larger, more complex genomes, thanks to recent advances in sequencing technology and bioinformatic approaches. It is also apparent that additional layers of complexity exist, such as the widespread horizontal transfer of TEs between different plant species [49], and even from parasitic arthropods to plants [50]. Further investigation of these processes in a larger array of

organismic interactions will provide valuable insights in coming years.

Finally, despite all potential benefits of TEs in evolutionary adaptation and optimized breeding, the dual nature of TEs as parasites and helpers should not be forgotten, and their blessings come along with a curse. The circumstances of transposon bursts, preferences of insertion sites, and the life cycle of many elements are not fully understood. Like in classical mutagenesis with chemical or physical treatments, unwanted side effects are likely and cannot be excluded, and new TE-related phenotypes must be thoroughly tested for genetic and epigenetic stability. However, detrimental and beneficial events can teach us both principles, and well-established advantageous interactions between TEs and genes might serve as templates for more precise and targeted genome editing and breeding.

Conflict of interest

The authors declare that no conflicts of interest exist.

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