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## Transposons: a blessing curse

Manu J Dubin<sup>1</sup>, Ortrun Mittelsten Scheid<sup>2</sup> and Claude Becker<sup>2</sup>

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.

### Addresses

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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.

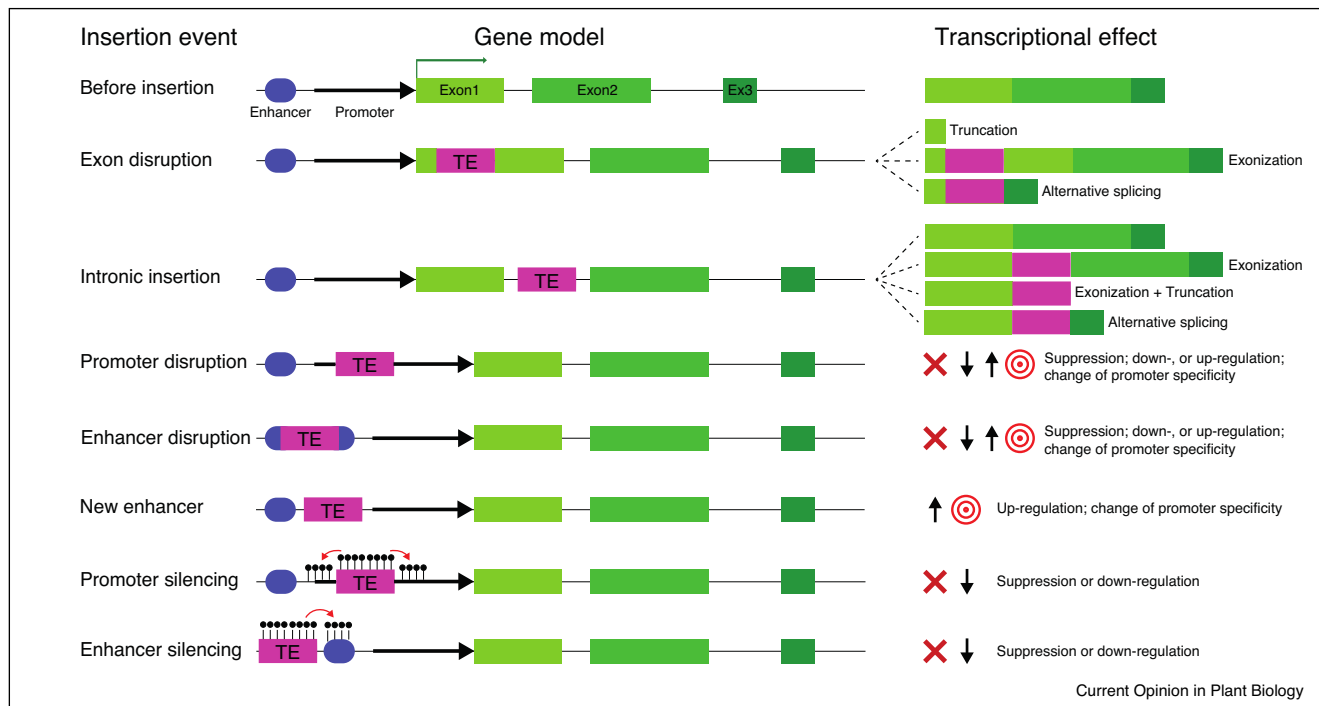
Plants have evolved intricate regulatory machineries to subdue TE mobility and to prevent transposition (recent reviews in [6–8]). Nonetheless, plant genomes carry signatures of massive TE bursts as well as of constant low-frequency transposition [9,10], and it has been postulated that some of these 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<sup>••</sup>] 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<sup>••</sup>]. 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<sup>••</sup>]. 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<sup>•</sup>]. 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<sup>••</sup>]. Even when located downstream of a protein-coding sequence, TEs can regulate gene expression: in *A. thaliana*, exposure to

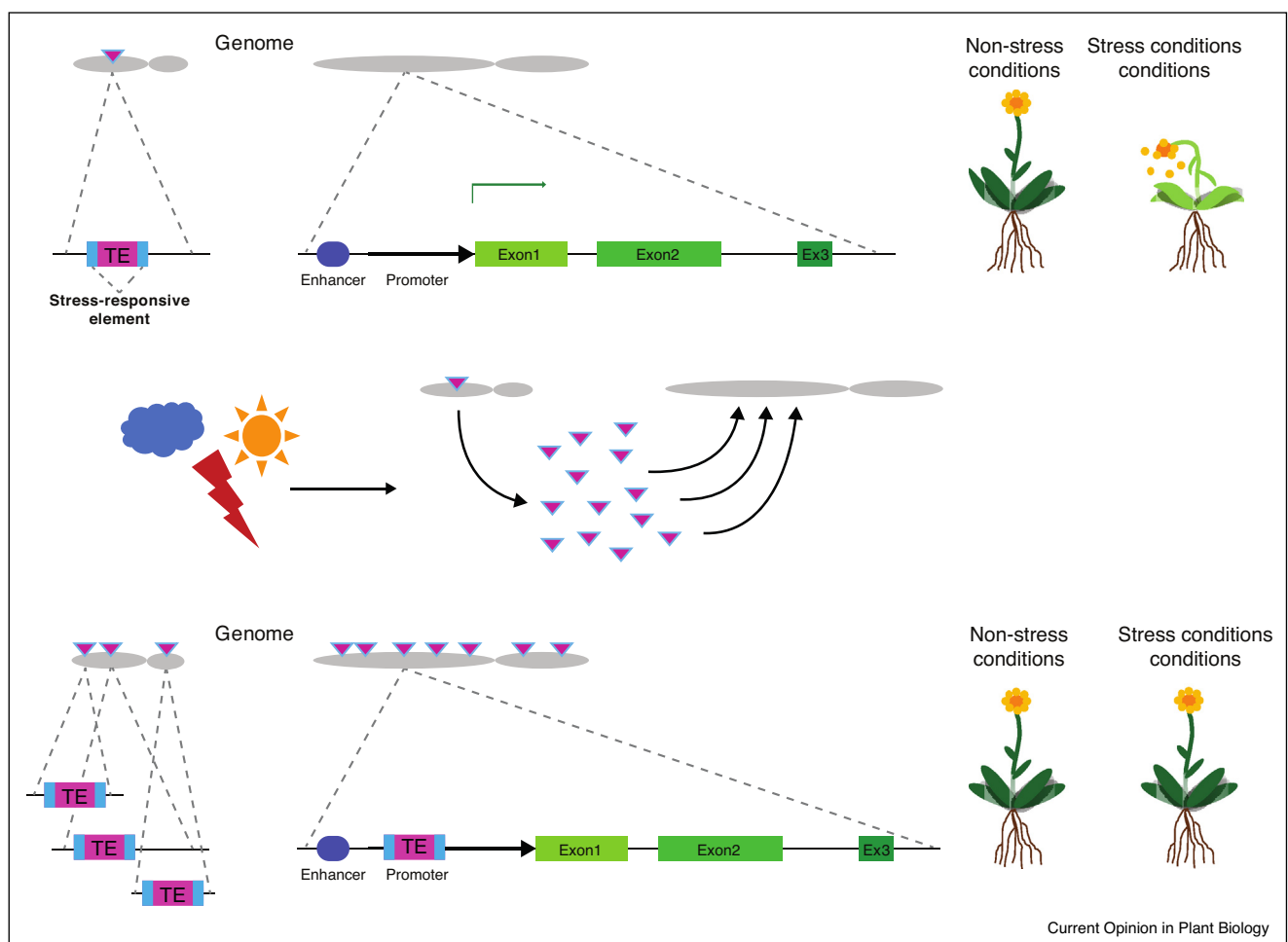
hyperosmotic stress resulted in loss of DNA methylation at a TE downstream of *CARBON NITROGEN INSENSITIVE 1 (CNI)* [26<sup>\*</sup>], in turn leading to the expression of an antisense long non-coding RNA (lncRNA) that is likely responsible for the down-regulation of the *CNI* sense transcript. A more 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<sup>\*\*</sup>]. 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<sup>\*\*</sup>]. 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<sup>\*\*</sup>]. 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].

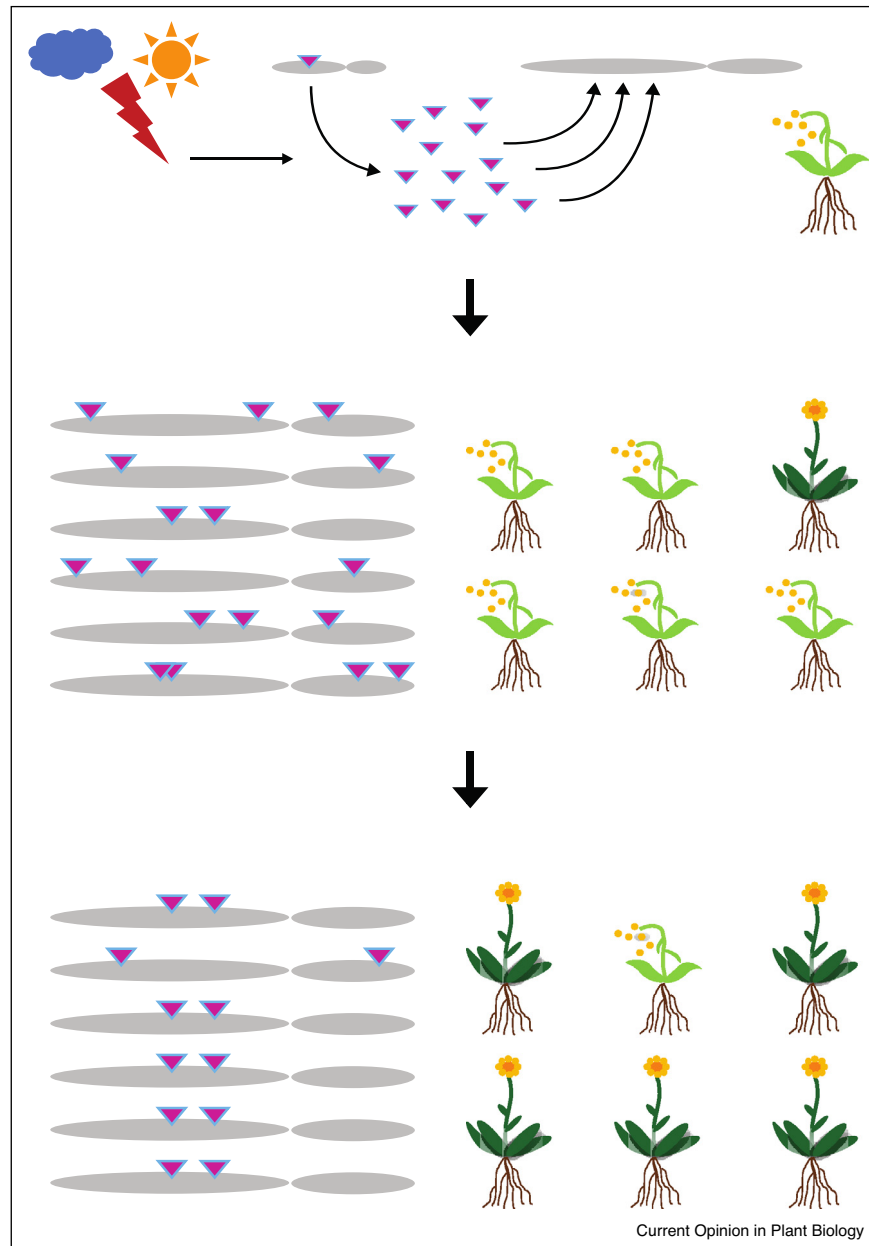
Recent studies have identified over 23 000 *de novo* TE gains and losses within a population of natural *A. thaliana* accessions [46<sup>\*\*</sup>,47<sup>\*\*</sup>]. New TE insertions generally occurred at low allele frequencies within the population, suggesting that the majority of events had been 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<sup>\*\*</sup>]. 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<sup>\*\*</sup>]. 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<sup>\*\*</sup>].

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<sup>\*</sup>]. 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<sup>\*</sup>].

### 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<sup>\*</sup>] and as a result of breeding efforts [35<sup>\*\*</sup>,48<sup>\*</sup>]. 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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### References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Wicker T, Sabot F, Hua-Van A, Bennetzen JL, Capy P, Chalhoub B, Flavell A, Leroy P, Morgante M, Panaud O *et al.*: **A unified classification system for eukaryotic transposable elements.** *Nat Rev Genet* 2007, **8**:973-982.
  2. Arabidopsis Genome Initiative: **Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*.** *Nature* 2000, **408**:796-815.
  3. Schnable PS, Ware D, Fulton RS, Stein JC, Wei F, Pasternak S, Liang C, Zhang J, Fulton L, Graves TA *et al.*: **The B73 maize genome: complexity, diversity, and dynamics.** *Science* 2009, **326**:1112-1115.
  4. Li X, Guo K, Zhu X, Chen P, Li Y, Xie G, Wang L, Wang Y, Persson S, Peng L: **Domestication of rice has reduced the occurrence of transposable elements within gene coding regions.** *BMC Genomic* 2017, **18**:55.
- The authors of this paper identify transposons in the genomes of three independently domesticated rice lines together with five wild relatives. They show that in each domestication event there is a dramatic loss of transposons from the coding region of genes and that transposons underlie many domestication loci in this species.
5. Song X, Cao X: **Transposon-mediated epigenetic regulation contributes to phenotypic diversity and environmental adaptation in rice.** *Curr Opin Plant Biol* 2017, **36**:111-118.
  6. Underwood CJ, Henderson IR, Martienssen RA: **Genetic and epigenetic variation of transposable elements in *Arabidopsis*.** *Curr Opin Plant Biol* 2017, **36**:135-141.
  7. Hirsch CD, Springer NM: **Transposable element influences on gene expression in plants.** *Biochim Biophys Acta* 2017, **1860**:157-165.

8. Fultz D, Choudury SG, Slotkin RK: **Silencing of active transposable elements in plants.** *Curr Opin Plant Biol* 2015, **27**:67-76.
  9. Maumus F, Quesneville H: **Ancestral repeats have shaped epigenome and genome composition for millions of years in *Arabidopsis thaliana*.** *Nat Commun* 2014, **5**:4104.
  10. Maumus F, Quesneville H: **Impact and insights from ancient repetitive elements in plant genomes.** *Curr Opin Plant Biol* 2016, **30**:41-46.
  11. McClintock B: **The significance of responses of the genome to challenge.** *Science* 1984, **226**:792-801.
  12. Lisch D: **How important are transposons for plant evolution?** *Nat Rev Genet* 2013, **14**:49-61.
  13. Sigman MJ, Slotkin RK: **The first rule of plant transposable element silencing: location, location, location.** *Plant Cell* 2016, **28**:304-313.
- This review highlights the importance of the genomic location of a transposon insertions site in determining its effect on gene regulation and on which the silencing pathways will act on it.
14. Ong-Abdullah M, Ordway JM, Jiang N, Ooi S-E, Kok S-Y, Sarpan N, Azimi N, Hashim AT, Ishak Z, Rosli SK *et al.*: **Loss of Karma transposon methylation underlies the mantled somaclonal variant of oil palm.** *Nature* 2015, **525**:533-537.
- The authors report that spontaneous loss of methylation at a transposon within the intron of a transcription factor underlies somaclonal variation in oil palm remarkable study of somaclonal variation causing mantled and thus agronomically useless fruits in oil palm.
15. Huang J, Gao Y, Jia H, Liu L, Zhang D, Zhang Z: **Comparative transcriptomics uncovers alternative splicing changes and signatures of selection from maize improvement.** *BMC Genomic* 2015, **16**:363.
  16. Cowley M, Oakey RJ: **Transposable elements re-wire and fine-tune the transcriptome.** *PLoS Genet* 2013, **9**:e1003234.
  17. Matzke MA, Mosher RA: **RNA-directed DNA methylation: an epigenetic pathway of increasing complexity.** *Nat Rev Genet* 2014, **15**:394-408.
  18. Xiao H, Jiang N, Schaffner E, Stockinger EJ, van der Knaap E: **A retrotransposon-mediated gene duplication underlies morphological variation of tomato fruit.** *Science* 2008, **319**:1527-1530.
  19. Martin A, Troadec C, Boualem A, Rajab M, Fernandez R, Morin H, Pitrat M, Dogimont C, Bendahmane A: **A transposon-induced epigenetic change leads to sex determination in melon.** *Nature* 2009, **461**:1135-1138.
  20. Butelli E, Licciardello C, Zhang Y, Liu J, Mackay S, Bailey P, Reforgiato-Recupero G, Martin C: **Retrotransposons control fruit-specific, cold-dependent accumulation of anthocyanins in blood oranges.** *Plant Cell* 2012, **24**:1242-1255.
  21. Castelletti S, Tuberosa R, Pindo M, Salvi S: **A MITE transposon insertion is associated with differential methylation at the maize flowering time QTL Vgt1.** *G3* 2014, **4**:805-812.
  22. Studer A, Zhao Q, Ross-Ibarra J, Doebley J: **Identification of a functional transposon insertion in the maize domestication gene *tb1*.** *Nat Genet* 2011, **43**:1160-1163.
  23. Yang Q, Li Z, Li W, Ku L, Wang C, Ye J, Li K, Yang N, Li Y, Zhong T *et al.*: **CACTA-like transposable element in *ZmCCT* attenuated photoperiod sensitivity and accelerated the postdomestication spread of maize.** *Proc Natl Acad Sci U S A* 2013, **110**:16969-16974.
  24. Mao H, Wang H, Liu S, Li Z, Yang X, Yan J, Li J, Tran L-SP, Qin F: **A transposable element in a NAC gene is associated with drought tolerance in maize seedlings.** *Nat Commun* 2015, **6**:8326.
- These authors demonstrate that natural variation in an agronomically important trait is caused by the insertion of a MITE element in the promoter of a transcription factor.
25. Secco D, Wang C, Shou H, Schultz MD, Chiarenza S, Nussbaum L, Ecker JR, Whelan J, Lister R: **Stress induced gene expression**



**drives transient DNA methylation changes at adjacent repetitive elements.** *eLife* 2015, 4:e09343.

These authors show that stress induces changes in methylation of TEs close to stress-induced genes, however the methylation changes occur after the transcription change suggesting that it is a downstream response.

26. Wibowo A, Becker C, Marconi G, Durr J, Price J, Hagmann J, Papareddy R, Putra H, Kageyama J, Becker J *et al.*: **Hyperosmotic stress memory in Arabidopsis is mediated by distinct epigenetically labile sites in the genome and is restricted in the male germline by DNA glycosylase activity.** *eLife* 2016, 5:e13546.
- This paper identifies DNA methylation changes in hyperosmotic stress changed plants and demonstrates that they can be transmitted to progeny, but only via the female germline.
27. Wang D, Qu Z, Yang L, Zhang Q, Liu Z-H, Do T, Adelson DL, Wang Z-Y, Searle I, Zhu J-K: **Transposable elements (TEs) contribute to stress-related long intergenic noncoding RNAs in plants.** *Plant J Cell Mol Biol* 2017, 90:133-146.
28. Bucher E, Reinders J, Mirouze M: **Epigenetic control of transposon transcription and mobility in Arabidopsis.** *Curr Opin Plant Biol* 2012, 15:503-510.
29. Casacuberta E, González J: **The impact of transposable elements in environmental adaptation.** *Mol Ecol* 2013, 22:1503-1517.
30. Yasuda K, Ito M, Sugita T, Tsukiyama T, Saito H, Naito K, Teraishi M, Tanisaka T, Okumoto Y: **Utilization of transposable element mPing as a novel genetic tool for modification of the stress response in rice.** *Mol Breed* 2013, 32:505-516.
31. Cavrak VV, Lettner N, Jamge S, Kosarewicz A, Bayer LM, Mittelsten Scheid O: **How a retrotransposon exploits the plant's heat stress response for its activation.** *PLoS Genet* 2014, 10:e1004115.
32. Ito H, Gaubert H, Bucher E, Mirouze M, Vaillant I, Paszkowski J: **An siRNA pathway prevents transgenerational retrotransposition in plants subjected to stress.** *Nature* 2011, 472:115-119.
33. Naito K, Zhang F, Tsukiyama T, Saito H, Hancock CN, Richardson AO, Okumoto Y, Tanisaka T, Wessler SR: **Unexpected consequences of a sudden and massive transposon amplification on rice gene expression.** *Nature* 2009, 461:1130-1134.
34. Pietzenek B, Markus C, Gaubert H, Bagwan N, Merotto A, Bucher E, Pecinka A: **Recurrent evolution of heat-responsiveness in Brassicaceae COPIA elements.** *Genome Biol* 2016, 17:209.
35. Makarevitch I, Waters AJ, West PT, Stitzer M, Hirsch CN, Ross-Ibarra J, Springer NM: **Transposable elements contribute to activation of maize genes in response to abiotic stress.** *PLoS Genet* 2015, 11:e1004915.
- This paper demonstrates that stress responsiveness of many genes is linked to nearby TE insertions. They identify 20 TE families that up-regulate genes in response to stress and 3 that downregulate them.
36. Paszkowski J: **Controlled activation of retrotransposition for plant breeding.** *Curr Opin Biotechnol* 2015, 32:200-206.
- This review documents known examples of TE transpositions to date and discusses the possible use of TEs for plant breeding.
37. Thieme M, Lanciano S, Balzergue S, Daccord N, Mirouze M, Bucher E: **Inhibition of RNA polymerase II allows controlled mobilisation of retrotransposons for plant breeding.** *Genome Biol* 2017, 18:134.
- These authors report that the combination of heat stress together with DNA demethylation agents or polymerase inhibitors is able to achieve robust activation and transposition of the heat responsive ONSEN TE. They further demonstrate that the progeny have altered phenotypes and suggest its use for plant breeding.
38. Hu TT, Pattyn P, Bakker EG, Cao J, Cheng J-F, Clark RM, Fahlgren N, Fawcett JA, Grimwood J, Gundlach H *et al.*: **The *Arabidopsis lyrata* genome sequence and the basis of rapid genome size change.** *Nat Genet* 2011, 43:476-481.
39. Seymour DK, Koenig D, Hagmann J, Becker C, Weigel D: **Evolution of DNA methylation patterns in the Brassicaceae is driven by differences in genome organization.** *PLoS Genet* 2014, 10:e1004785.
40. Willing E-M, Rawat V, Mandáková T, Maumus F, James GV, Nordström KJV, Becker C, Warthmann N, Chica C, Szarzynska B *et al.*: **Genome expansion of *Arabidopsis lyrata* linked with retrotransposition and reduced symmetric DNA methylation.** *Nat Plants* 2015, 1:14023.
41. Lockton S, Gaut BS: **The evolution of transposable elements in natural populations of self-fertilizing *Arabidopsis thaliana* and its outcrossing relative *Arabidopsis lyrata*.** *BMC Evol Biol* 2010, 10:10.
42. de la Chaux N, Tsuchimatsu T, Shimizu KK, Wagner A: **The predominantly selfing plant *Arabidopsis thaliana* experienced a recent reduction in transposable element abundance compared to its outcrossing relative *Arabidopsis lyrata*.** *Mob DNA* 2012, 3:2.
43. Agren JÅ, Wang W, Koenig D, Neuffer B, Weigel D, Wright SI: **Mating system shifts and transposable element evolution in the plant genus *Capsella*.** *BMC Genomic* 2014, 15:602.
44. Staton SE, Burke JM: **Evolutionary transitions in the Asteraceae coincide with marked shifts in transposable element abundance.** *BMC Genomic* 2015, 16:623.
45. Mascagni F, Barghini E, Giordani T, Rieseberg LH, Cavallini A, Natali L: **Repetitive DNA and plant domestication: variation in copy number and proximity to genes of LTR-retrotransposons among wild and cultivated sunflower (*Helianthus annuus*) genotypes.** *Genome Biol Evol* 2015, 7:3368-3382.
46. Stuart T, Eichten SR, Cahn J, Karpievitch YV, Borevitz JO, Lister R: **Population scale mapping of transposable element diversity reveals links to gene regulation and epigenomic variation.** *eLife* 2016, 5:e20777.
- See also [47\*]. These authors document over 23 000 TE gains/losses in a population of approximately 200 *Arabidopsis thaliana* accessions. They demonstrate that many of these gains/losses are associated with changes in gene expression and are not in linkage-disequilibrium with the surrounding SNPs and as such represent an additional source of variation not picked up using conventional marker based methods.
47. Quadrana L, Bortolini Silveira A, Mayhew GF, LeBlanc C, Martienssen RA, Jeddalo JA, Colot V: **The *Arabidopsis thaliana* mobilome and its impact at the species level.** *eLife* 2016, 5:15716.
- See also [46\*]. Using the same population of *Arabidopsis thaliana* accessions these authors also identify gains and losses of TEs in this population. They identify TEs whose abundance is linked to the climate from which they originate. They also suggest that in some cases early flowering in this species is caused by TE insertions in the vicinity of flowering time genes.
48. Lai X, Schnable JC, Liao Z, Xu J, Zhang G, Li C, Hu E, Rong T, Xu Y, Lu Y: **Genome-wide characterization of non-reference transposable element insertion polymorphisms reveals genetic diversity in tropical and temperate maize.** *BMC Genomic* 2017, 18:702.
- These authors document over 250 000 TE gains/losses in a population of maize lines and show that they may be involved in adaptation to temperate climates.
49. El Baidouri M, Carpentier M-C, Cooke R, Gao D, Lasserre E, Llauro C, Mirouze M, Picault N, Jackson SA, Panaud O: **Widespread and frequent horizontal transfers of transposable elements in plants.** *Genome Res* 2014, 24:831-838.
50. Gao D, Chu Y, Xia H, Xu C, Heyduk K, Abernathy B, Ozias-Akins P, Leebens-Mack JH, Jackson SA: **Horizontal transfer of non-LTR retrotransposons from arthropods to flowering plants.** *Mol Biol Evol* 2017 <http://dx.doi.org/10.1093/molbev/msx275>.