

REVIEW

Genomics, Molecular Genetics & Biotechnology

Transposable elements: Functional aspects and applications as drivers of crop innovation

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Abstract

Transposable elements (TEs), which were once relegated to the status of genomic parasites, are today accepted as important agents of plant genome evolution and adaptation. This review integrates evidence pointing to their dual function as drivers of genetic diversity and instability, with a focus on their contribution to phenotypic innovation, stress tolerance, and crop trait control. TEs create structural and regulatory diversity by insertional mutagenesis, *cis*-regulatory sequence donation, and epigenetic interactions, facilitating fast adaptation to environmental stress. Advances in omics technologies have unraveled TE dynamics, showing insertion bias toward genic and regulatory regions and stress-responsive activation patterns. The influence of the mobilome on crop improvement is emphasized by TE-derived molecular markers, clustered regularly interspaced short palindromic repeats-mediated TE regulation, and epigenome editing that minimizes risks of genome instability while tapping TE-driven diversity. Rice (*Oryza sativa* L.) *mPing* and maize (*Zea mays* L.)

Abbreviations: AI, artificial intelligence; CRISPR, clustered regularly interspaced short palindromic repeats; DDM1, decreased in DNA methylation 1; DSBs, double-strand breaks; GWAS, genome-wide association studies; LINE, long interspersed nuclear element; lncRNA, long non-coding RNA; LTR, long terminal repeat; miRNA, microRNA; MITE, miniature-inverted-repeat transposable element; ncRNA, non-coding RNA; NGS, next-generation sequencing; Pol II, polymerase II; RdDM, RNA-directed DNA methylation; RISC, RNA-induced silencing complex; RNAi, RNA interference; siRNA, small interfering RNA; TGS, transcriptional gene silencing; TIPS, transposon insertion polymorphisms; TSS, transcription start site; UTR, untranslated regions.

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Hopscotch, for instance, demonstrate TE potential in trait enhancement and domestication. Moreover, multi-omics integration has defined TEs' input into stress response and genome plasticity, offering new targets for precision breeding. Challenges remain in modeling TE behavior and weighing adaptive potential against harmful effects, requiring sophisticated computational models and synthetic biology strategies. Interdisciplinary approaches integrating machine learning and synthetic TE design should be prioritized in future research to maximize TE-mediated crop resilience. With the integration of TE biology and cutting-edge biotechnologies, global food security issues, fueled by climate change, can be mitigated by the scientific community. This overview situates TEs not merely as genomic leftovers but as essential next-generation crop requirements, necessitating their strategic location in sustainable agro-innovation.

Plain Language Summary

Transposable elements (TEs) are small pieces of DNA that can move around within plant genomes. Once thought to be useless “junk DNA,” they are now recognized as key players in creating genetic diversity, shaping evolution, and influencing how plants respond to their environment. This review brings together past and recent studies to explain how TEs work and why they matter. We show that TEs can change gene activity, act as switches for important traits, and even help plants adapt to stress. Our article goes beyond biology, exploring how TEs can be used in crop breeding and biotechnology to build climate-resilient crops and improve food security. The key message is that TEs are not just disruptors but powerful tools that scientists can harness to develop better crops for future challenges.

1 | INTRODUCTION

Growing demands for sustainable agri-productivity, driven by the cumulative effect of climate change and the ever-increasing world population, placed crop improvement at the global food security crossroads (Ray et al., 2013). Both conventional breeding approaches and recent genomic-assisted tools aim to use genetic variation to generate more efficient and resilient varieties. However, the genetic mechanisms of innovation in plant genomes, particularly those responsible for rapid adaptation and phenotypic diversification, are only partially understood. In this manner, transposable elements (TEs), once scorned as “junk DNA,” have taken center stage in plant evolution and adaptation (Roquis et al., 2021).

TEs are mobile DNA sequences capable of moving within the genome, where they can induce mutations, restructure genes, and modulate gene expression. Since Barbara McClintock's seminal finding in maize (*Zea mays* L.) (McClintock, 1950), the scientific perception of TEs has been radically reshaped—transformation from genetic curiosities to dynamic forces of genomic innovation. Enough evidence is

now available to persuade us that TEs activity can modulate gene expression and significantly affect agronomic traits such as stress tolerance (Bennetzen & Wang, 2014), flowering time (Song et al., 2020), fruit shape (Butelli et al., 2012), and disease resistance (X. Cui & Cao, 2014). However, their dual role as both drivers of adaptability and sources of genomic instability has slowed their direct application in breeding programs.

New genomics, epigenomics, and bioinformatics research are illuminating how TEs contribute to functional plant diversity. In rice (*Oryza sativa* L.) populations, for instance, scientists have confirmed that TE activation can generate new genetic variations for environmental adaptation (Castanera et al., 2023). In tomato (*Solanum lycopersicum* L.), the promoter of the gene *LE-ACS7* (coding an ACC synthase, a key enzyme of ethylene biosynthesis) was tagged by a *Sol3* transposon. This entity is also present in the tomato polygalacturonase promoter, to which it conferred regulatory elements. It was suggested that *Sol3* transposons affect the regulation of *LE-ACS7* (Shiu et al., 1998). The researchers hypothesized that TEs have increased the flexibility of the

tomato ethylene biosynthetic machinery, potentially contributing to root-to-shoot signaling in waterlogged plants. The mentioned cases illustrate how genomic plasticity induced by TEs can be utilized to accelerate the process of generating cultivars that are more resilient to environmental stressors.

Such findings are increasingly paving the way for the use of TEs as functional tools in crop improvement. Clustered regularly interspaced short palindromic repeats (CRISPR)-related technologies, for example, are being explored for the modulation of TE activity and controlling their integration into genomic targets with adaptive potential (Tenjo-Castaño et al., 2023). One pivotal challenge for TE-based genome engineering is dealing with large-sized TEs, which are well documented in eukaryotes (Arkhipova et al., 2019). Larger TEs increase the total DNA cargo, additional sequences such as genes, open reading frames (ORFs), or regulatory elements that must be mobilized. A potential way to overcome this challenge is working with minimalized systems. For instance, P. Liu et al. (2024) developed a system based on *Pong* transposase proteins and reprogrammable nucleases such as Cas9. They demonstrated that this system can carry cargos ranging from very small (~444 bp) to very large (~9 kb). Insertion efficiency remained high (~26%–28%) for cargos around 1–1.5 kb but decreased to 8.3% when the cargo approached 8.6 kb, indicating a clear size-dependent reduction. Concurrently, population genomics research is enabling the identification of allelic variants generated by TEs, offering candidate targets for marker-assisted selection. However, there are overwhelming challenges for such applications, including accurate prediction of TE behavior and controlling undesirable outcomes generated by unprogrammed activation.

This article investigates the various roles played by TEs, including their functional attributes and biotechnological possibilities for crop innovation. We synthesize current advances and strategic aspects across a range of interconnected topics, including (i) TEs as plant genetic diversity drivers, and positional effects and insertional biases; (ii) roles in gene regulation; (iii) epigenetic control of TE activity; (iv) omics-based approaches to uncover TE dynamics; (v) the plant mobilome and its implications for breeding; (vi) TE-mediated modulation of specific genes; (vii) their newly emerging role in climate resilience; and (viii) the future of TE-based technologies.

Comprehensive understanding of these factors is crucial for converting their diversity-generating potential into effective applications for sustainable agriculture. Along the way, this work seeks to offer the scientific community a synoptic and prospective picture of a strategic and yet underdeveloped field in plant biology.

Core Ideas

- Transposable elements (TEs) are drivers of genomic instability and genetic variability.
- The range of phenotypic effects can be harvested for crop breeding purposes.
- Multi-omics contribute to TE biology understanding and effects in the host genome.
- Stress-responsive TEs may drive agronomic trait variation under climate change.
- Synthetic biology and artificial intelligence (AI) offer new ways to harness TEs for crop resilience.

2 | SHORT HISTORICAL PERSPECTIVE ON TEs AS DRIVERS OF GENETIC DIVERSITY

Genetic diversity is a key component in plants' adaptation to environmental changes or any other threat to population's survival (Chung et al., 2023; Hoffmann et al., 2021). This plurality arises from mutations, recombination, gene flow, and evolutionary forces such as genetic drift, while natural selection acts upon this diversity, shaping the adaptive potential of populations. TEs also act as drivers of diversity, especially given their ability to regulate gene expression.

Barbara McClintock's groundbreaking study proposed that "mutable loci" were able to control gene expression influencing phenotypic traits like variegated kernels in maize (McClintock, 1950) (Figure 1). For several years, this work was neglected, but it is now recognized as the foundation of TE studies. Another important landmark was the discovery of reverse-transcriptase in retroviruses, which challenged the central dogma of biology and laid the foundation for understanding the transposition mechanism in the early 1970s and late 1980s. Meanwhile, research focused on explaining hybrid dysgenesis in *Drosophila melanogaster* finally associated these effects with the mobilization of specific TEs (P elements and I elements) (Kidwell, 1979) (Figure 1).

The mutable loci, called Ac (Activator) and Ds (Disso-ciator), also were sequenced in maize (Döring et al., 1984) (Figure 1). P elements in *Drosophila* and Ac elements in maize were characterized as what we now call DNA transposons (Figure 1), according to the classification proposed by Wicker et al. (2007). With the findings of Boeke et al. (1985) that Ty1 elements in yeast were able to transpose through an RNA-mediated action, the term "retrotransposon" was proposed (Figure 1). Concurrently, transposon tagging, a genetic technique used to isolate genes by using a mobile DNA

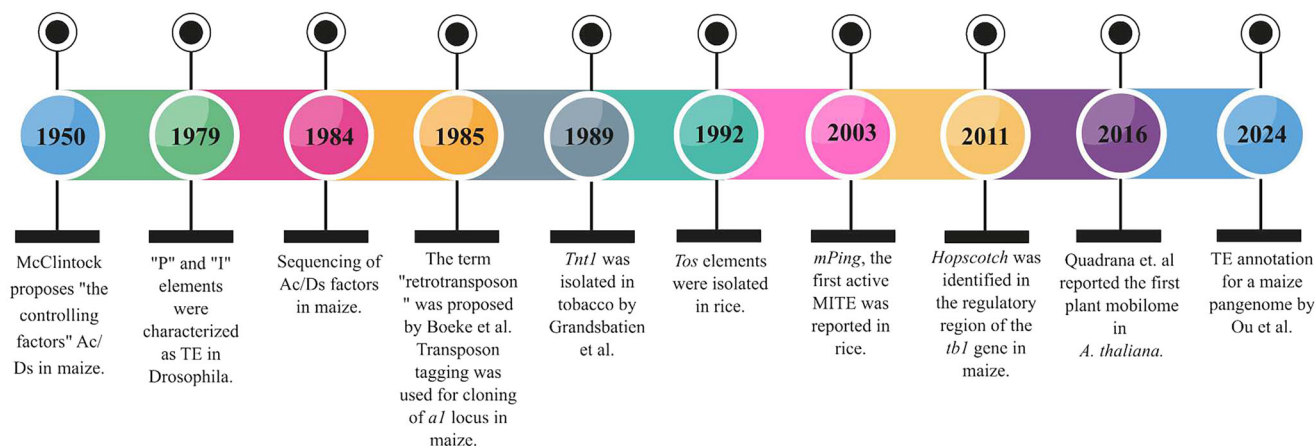


FIGURE 1 Timeline with main milestones in transposable element studies.

sequence, was broadly employed, especially for Ac/Dc and mutator TEs. These early transposon tagging studies, particularly in maize, demonstrated that TEs had a profound impact on agronomically important traits way before the genomic era. Representative examples include the cloning of the *al* locus, involved in anthocyanin biosynthesis and kernel pigmentation (O'Reilly et al., 1985) (Figure 1), the isolation of *opaque-2* (*o2*), a key regulator of endosperm protein synthesis identified through visually scorable transposon-induced mutants (Schmidt et al., 1987), and the cloning of *sugary1* (*su1*), which encodes an isoamylase required for proper starch biosynthesis and whose mutation alters starch composition and sugar content in kernels, a trait widely exploited in sweet corn breeding (James et al., 1995). In the 1990s, the first active retrotransposon, *Tnt1*, was isolated in tobacco (*Nicotiana tabacum* L.) (M. Grandbastien et al., 1989) (Figure 1). In this work they showed that *Tnt1* transposed during cell culture and inserted into nitrate reductase gene, which made it possible to identify it and characterize it as a long terminal repeat (LTR). Retrotransposons were isolated in plants using Southern blotting to visualize the LTRs of the *Tos* family in *O. sativa* (Hirochika et al., 1992) (Figure 1). A few years later, the first active DNA transposon from the miniature-inverted-repeat transposable element (MITE) family, called *mPing*, was simultaneously reported in rice (Jiang et al., 2003; Kikuchi et al., 2003; Nakazaki et al., 2003) (Figure 1). Since the rise of next-generation sequencing (NGS) technologies in the 2000s, the increased availability of genomic data has allowed for more in-depth exploration of how TEs influence gene expression. For example, the insertion of *mPing*, was reported in rice and led to up-regulation of gene transcription (Naito et al., 2009), supporting previous hypotheses that TEs and other repetitive sequences could mediate gene expression. Another example is the element *Hopscotch*, reported in the regulatory region of the *tb1* gene in maize (Figure 1).

This element acted as an enhancer of gene expression and could partially explain the apical dominance in comparison to teosinte (the wild ancestor of maize, also known as guinea corn), which facilitated maize domestication (Studer et al., 2011). Following that, Quadrana et al. (2016) reported the first plant mobilome (the entire set of mobile genetic elements in a genome) while studying the *Arabidopsis thaliana* (L.) Heynh genome (Figure 1). They highlighted important information for current understanding of TEs' roles, such as their pericentromeric insertion preference, regulation on nearby gene expression, and impact on the DNA methylation status of adjacent sequences (see Section 4.3).

More recently, the increasing availability of accurate TE-annotation pipelines has made it possible to systematically compare TE content at a pangenome level. For instance, Ou et al. (2024) compared 26 maize reference genomes from two groups: tropical and temperate maize. They reported that tropical maize genomes had 35 Mb more than temperate and that this difference is driven by few young LTR families (Figure 1). Similarly, a pangenome analysis of potatoes (*Solanum* spp.) from section *Petota* revealed a high TE content (75.5%) (Bozan et al., 2023). Based on presence/absence variation, a phylogenetic tree was constructed separating these genomes in clades. Notably, the highest number of TE-related genes was detected in a clade composed predominantly of accessions derived from in vitro culture, suggesting TE activation in this type of propagation. The study further proposes that TE activation may have contributed to genome and taxonomic diversification in *Petota* species during their expansion into new environments (Bozan et al., 2023).

In summary, once neglected, TEs are now recognized as important contributors to genetic diversity and evolution. In a short window of time, groundbreaking discoveries were made in plants, and the ways in which TEs impact specific traits are becoming clearer.

3 | THE DYNAMICS OF TES AND THEIR GENOMIC IMPACTS

The dynamics of TEs play a central role in shaping genome architecture. TEs drive genetic diversity by inducing mutations, causing genomic rearrangements, and generating novel regulatory and expression networks. Understanding these processes is essential for explaining their contribution to evolution, adaptation, and the genetic improvement of agronomically important species. Key aspects of the TEs' dynamics and their impact on the genomes are explored in the following sections.

3.1 | TEs insertional preferences are not totally random

The “jumping” sequences are much more than sequences that randomly change location; the specific sites where transposition occurs are crucial for understanding their impact on the plant genome. While several TE families tend to integrate near protein-coding genes or transcription start sites (TSSs), this pattern is far from universal, particularly among plant LTR retrotransposons, which can also target heterochromatic regions (Lippman et al., 2004). It is important to acknowledge a discovery bias when discussing TE insertions in genes. Many TEs were first described because they caused visible or selectable phenotypes, for example, in the work by Studer et al. (2011), making gene-targeting insertion events easier to detect. Consequently, elements inserting into intergenic or silent regions were less likely to be isolated and studied. Although genuine insertion preferences exist, this methodological bias should be considered when interpreting TE–gene associations. Population-level studies reinforce this heterogeneity: in maize, whole-genome profiling of 509 diverse inbred lines uncovered different TE insertion sites, spanning both genic and intergenic regions (Qiu et al., 2021).

Regarding TE insertional preferences, some LTR retrotransposons integrate near TSS or within genes, where RNA polymerase II (Pol II) activity and chromatin remodeling create a favorable environment for their insertion and potential activation (Lisch, 2013; R. K. Slotkin & Martienssen, 2007). X. Zhang et al. (2020) investigated TE target site distribution in different eukaryotic genomes, including maize and rice, and compared them in the context of genome-wide transcriptional landscapes. Through this work, they proposed two distinct strategies for TE insertion: Type-A, which is characterized by a strong association between TE integration and the initiation of transcription by Pol II as well as some TEs families enriched in TSS regions. In contrast, Type-B Strategy shows a broader targeting pattern, being enriched near both TSSs and transcription termination sites of genes that are expressed

at medium levels. From the perspective of TEs, these strategies increase their chances of transcription and propagation. At the same time, they help minimize potential harm to the host genome—an important balance, given that TEs maintain a kind of symbiotic relationship with their host. As a matter of fact, target site preference is part of TE–host co-adaptation strategies that can lead to either TE repression, for example, via DNA methylation, or TE reactivation (Sultana et al., 2017).

Plant TEs tend to insert in open euchromatic regions adjacent to genes, open chromatin, and centromeric/pericentromeric regions (Figure 2a), as observed in maize and *Arabidopsis* spp. (Catlin & Josephs, 2022). Chromatin accessibility facilitates transposases (for DNA transposons) or reverse transcriptase and integrases (for retrotransposons) to recognize and insert more efficiently. However, older TEs might occur in heterochromatic regions (Figure 2a), where they are generally not negatively selected (R. K. Slotkin & Martienssen, 2007). As a matter of fact, TEs biased toward centromeric and pericentromeric regions contribute to structural organization and genome stability. Among the major components in pericentromeric regions, LTRs Ty1/Gypsy and Ty3/Copia stand out (Gao et al., 2015; Papolu et al., 2022). Insertions in heterochromatin regions are often silenced by epigenetic mechanisms such as DNA methylation. For example, *A. thaliana* TE mobility is under the control of decreased in DNA methylation 1 (DDM1), a key gene for the regulation of chromatin structure and DNA methylation levels (Lippman et al., 2004). Epigenetic mechanisms will be addressed later in this review (see Section 4.3).

3.2 | TEs as influential neighbors: A focus on their insertional effects

The role of TEs in gene regulation is crucial for creating genetic diversity due to the range of phenotypic effects these elements insertions can cause. It is important to highlight their tendency to insert nearby genes, as an attempt to propagate in the host genome without causing deleterious effects in the host population (Munasinghe et al., 2023). Changes in gene expression can be related to where the transposition or retrotransposition happened (Hirsch & Springer, 2017). TE insertion in promoter or enhancer regions can either activate or silence gene expression, as seen in grape (*Vitis vinifera* L.) skin color (Kobayashi et al., 2004). This trait depends on the expression of the regulatory gene *VvMYB1*, a MYB-type transcription factor that activates the anthocyanin biosynthesis pathway. Kobayashi et al. (2004) demonstrated that white cultivars carry a full-length *Gret1* insertion—a LTR-retrotransposon—in the *VvMYB1* promoter, which

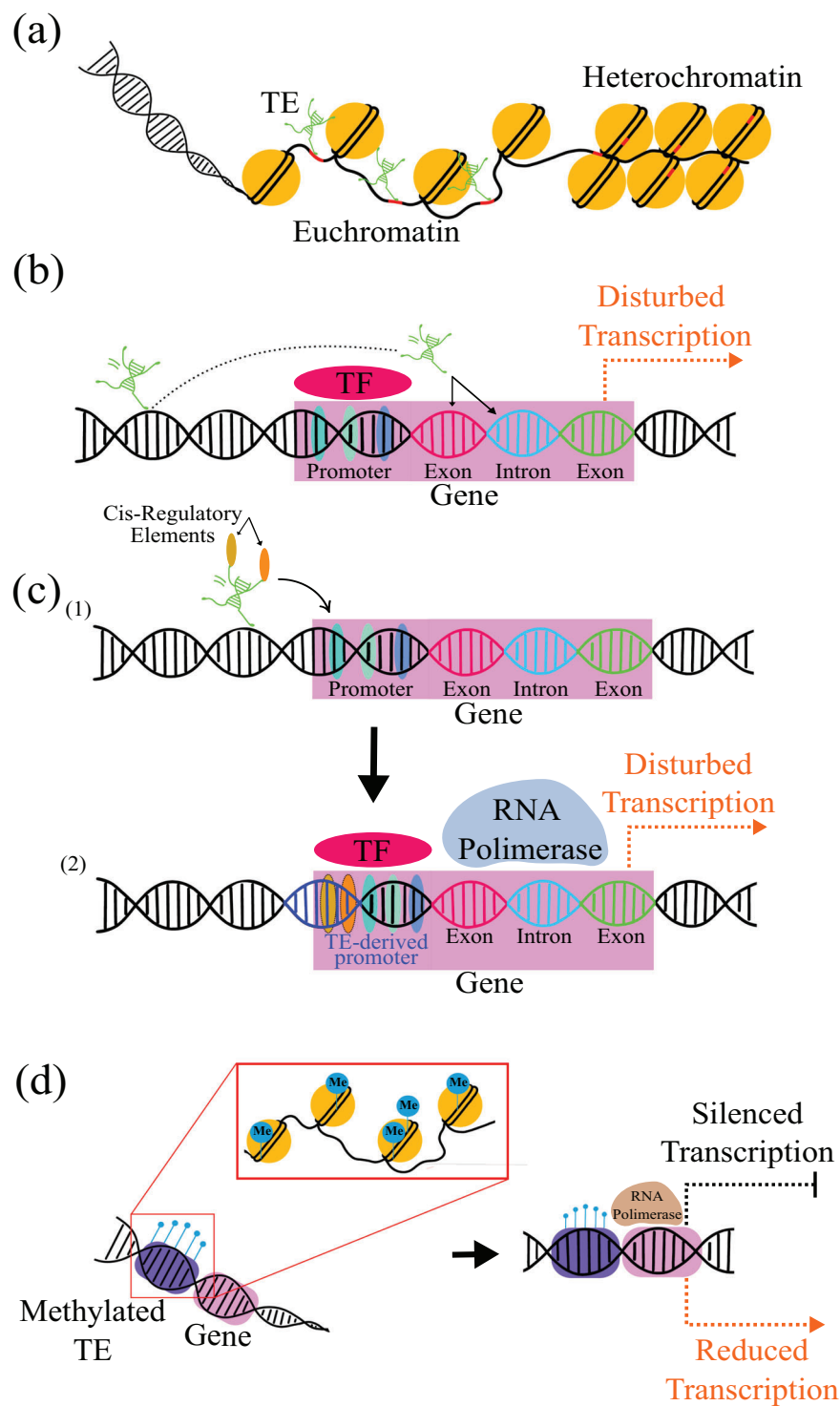


FIGURE 2 Transposable elements (TEs) dynamics and effects on plant genome. (a) Insertional preferences in open euchromatic regions and heterochromatic regions. (b) Exonic insertions can disturb transcription resulting in nonfunctional proteins or create novel protein isoforms through alternative splicing. Alternatively, intronic insertions could proliferate without major impacts on the genome but eventually alter gene expression levels or alternative splicing. (c) TE role in gene regulation, c-1. TE containing their own *cis*-regulatory elements inserted in the promoter/enhancer region of the gene; c-2. After the insertion, the transposable element donates its *cis*-regulatory sequences, resulting in a new TE-derived promoter region that can alter expression levels and create new gene regulatory networks and novel phenotypic traits. (d) Epigenetic silencing of TEs nearby genes, as an attempt to avoid TEs deleterious effects. However, this control over TEs can spread to nearby genes, repressing or reducing their expression levels. TF, transcript factor.

suppresses its transcription and results in the white skin phenotype.

TE insertions can occur within intragenic regions, which correspond to introns and exons (Figure 2b). Insertion in exons can disrupt the coding sequence, resulting in nonfunctional proteins or creating novel protein isoforms through alternative splicing (Catlin & Josephs, 2022; Gebrie, 2023; Hirsch & Springer, 2017) (Figure 2b). A classic example is the study in maize by Varagona et al. (1992), which showed that the Ds TE could be inserted into the exonic regions of the waxy (*wx*) gene, leading to its inactivation. Interestingly, the inserted TE was spliced out of the RNA transcript, allowing restoration of the functional integrity of the *wx* gene transcript. Also, in maize, the insertion of the LTR retrotransposon *ZmRE-1* into the fifth exon of the brachytic2 (*Br2*) allele (a protein that encodes an ATP-binding cassette phosphoglycoprotein and functions in polar auxin transport in maize stalk) led to the loss of normal transcript and reduced the transcript expression, which the authors speculate has the potential to change plant height without changing grain yield, considered two important characteristics for plant breeding purposes (C. Li et al., 2020).

If the insertion happens in intronic or untranslated regions (UTR), there's a tendency to TE settlement without majorly impacting the host genome, although significant changes in expression levels or alternative splicing may happen (Gebrie, 2023; Hirsch & Springer, 2017) (Figure 2b). An example of insertion in the 3' UTR was reported in which a CACTA transposon was inserted 10 bp downstream of the stop codon of the *LsGLK*, a candidate gene to the variation of dark- and pale-green leaves in lettuce (*Lactuca sativa* L.). This event resulted in alternative splicing, as observed by a significant reduction of functional *LsGLK* transcripts, causing a decrease in chlorophyll content and leading to the development of pale-green leaves (L. Zhang et al., 2022). There is also evidence in maize of DNA transposon MULE inserting in the intronic region of the alcohol dehydrogenase (*Adh1-S*) gene, resulting in new splice variants, and that these insertions are likely to diminish expression in many genes (Luehrsen & Walbot, 1990). Another example comes from a study in winter wheat (*Triticum aestivum* L.), which investigated whether the cold-induced expression of the wheat *VRN-A1* gene was associated with changes in DNA methylation. Khan et al. (2013) identified a TE inserted within an intron of *VRN-A1*, which was associated with altered non-CG DNA methylation under cold exposure.

TE exonization is also a possible outcome, occurring when a TE located in an intronic region becomes integrated within the coding sequence to be transcribed as an additional exon (Gill et al., 2021). This process reflects the co-option of TE sequences by the host genome, as seen in triticale where evidence of frequent exonization of Class I and Class II elements suggests a direct role for TEs in shaping the

structure and origin of long non-coding RNAs (lncRNAs) (Kirov, 2023).

3.3 | TEs and genomic instability: A double-edged sword

TEs have been acknowledged in genome evolution and regulatory innovation; however, their mobilization can also disrupt genome integrity (Bhat et al., 2022; Hedges & Deininger, 2007), as seen in humans in which TE mobilization has been repeatedly correlated to important diseases (Hancks & Kazazian, 2016). In this context, the term “genomic instability” can be caused by TE insertion within regulatory and/or coding sequences resulting in aberrant gene expression (loss of function or abnormal gene expression) (Hirsch & Springer, 2017), TE-mediated homologous recombination and chromosomal rearrangements such as deletions, duplications, and inversions (Gray, 2000).

TE insertions may disrupt coding sequences, as they are generally mutagenic and can lead to gene loss-of-function (Hirsch & Springer, 2017) (Figure 2b). A classic example is the famous pea (*Pisum sativum* L.) phenotypes described in Gregor Mendel's studies. Bhattacharyya et al. (1990) discovered that wrinkled seeds resulted from a mutation in a gene that encodes the starch-branching enzyme crucial for starch synthesis. The mutation is caused by a transposon-like sequence and leads to a nonfunctional enzyme responsible for wrinkled appearance due to an osmotic imbalance between sugar and starch. Another example was the study performed in the pangenome of oil rapeseed (*Brassica napus* L.) to understand the flowering time variation in different ecotypes (spring, winter, and semi-winter rapeseeds) (Song et al., 2020). The authors reported that a loss-of-function mutation was caused by a long interspersed nuclear element (LINE) insertion in the first exon of the *BnaA10.FLC* gene (associated with flowering time and ecotype variation), leading to a reduced or absent vernalization requirement in spring varieties. This insertion likely disrupted gene function by truncating transcripts through premature termination or by producing nonfunctional proteins. In contrast, a MITE insertion in the promoter gene's region was associated with increased expression and a strong vernalization in winter varieties (Song et al., 2020).

Plant genome integrity can also be disturbed by recombination of the homologous sequences or by faulty repair of double-strand breaks (DSBs) formed during TE excision using ectopic homologous sequences (Gray, 2000). This was demonstrated by Shalev and Levy (1997), who showed that the presence of the *Ac* element can induce ectopic homologous recombination in somatic plant cells. Additionally, in maize, a study demonstrated that DSBs were frequent in all chromosome regions, including centromeric and

pericentromeric regions, and most DSBs were composed of TEs, predominantly *Gypsy* retrotransposons (Y. He et al., 2017). Chromosomal rearrangements caused by TEs have been reported in different plant species. Recently, a transposon-mediated chromosomal rearrangement was reported to alter the gene expression profiles of the maize *p1* and *p2* genes, which encode MYB-homologous regulators of the flavonoid biosynthetic pathway, responsible for red pigmentation in floral organs (Sharma & Peterson, 2023). They demonstrated that *Ac/fAc* elements induced sequential duplication and relocations that moved the *p1* gene enhancer closer to the *p2* gene, inducing the *p2* gene in the pericarp and resulting in a red kernel pericarp phenotype. In rice, the *Ac/Ds* transposon system has been effectively employed to induce chromosomal rearrangements (Xuan et al., 2011, 2016).

To avoid possible deleterious effects, TE activity is often controlled by host defense mechanisms, including DNA methylation and small RNA pathways (see Section 4.3). Therefore, TE activity is a double-edged sword: in spite of possible deleterious effects, TE insertions can still generate genetic diversity that can be beneficial or subject to natural selection.

4 | HOW CAN TEs INFLUENCE GENE EXPRESSION?

In the past, there was a misconception that TEs were “junk DNA,” which is opposite to the current perspective of TEs as drivers of genetic diversity (Castanera et al., 2023; Catlin & Josephs, 2022; Grzebelus, 2018). Growing evidence supports TEs’ role in modulating gene expression (Mao et al., 2015; Quadrana, 2020), particularly by inserting near or within genes. In this section, we will dissect the ways TEs can influence transcriptional and post-transcriptional activity. Additionally, we will also discuss the epigenetic landscape, considering that TEs can also modulate nearby genes. Together, these mechanisms illustrate the multifaceted ways in which TEs contribute to gene regulation.

4.1 | TEs as *cis*-regulatory elements

TEs can act as “pseudo-promoters,” as they often carry multiple *cis*-regulatory sequences (Figure 2c.1), including sense and antisense promoters, splice donor and acceptor sites, and polyadenylation signals. By possessing their own *cis*-regulatory sequences, TEs can drive transcription across various regions of eukaryotic genomes while also providing *cis*-regulatory innovations to their host (Sundaram & Wysocka, 2020). Consistent with this view, a comparative analysis across plant species revealed that TEs located near stress-responsive genes frequently harbor overrepresented

cis-regulatory motifs (Deneweth et al., 2022). LTR/*Gypsy* TEs adjacent to genes were up-regulated under proteotoxic stress and enriched with motifs recognized by HSF2A transcription factors (involved in heat and proteotoxic stress in *A. thaliana*). Similarly, in tomato, Harbinger TEs located near light stress-responsive genes were found to contain motifs for MYB transcription factors, known as key regulators of light signaling and stress adaptation (Deneweth et al., 2022).

TE-derived regulatory motifs contribute to the emergence of new transcriptional responses and phenotypic variation. This is illustrated by transposon-associated polymorphisms in the promoters of nine stress-responsive genes across *A. thaliana* accessions. This work revealed regulatory diversity underlying differential stress adaptation (Naydenov et al., 2018). Additionally, in tobacco, a 13-bp motif within the LTR promoter of *Tto1* conferred responsiveness to tissue culture, wounding, and methyl jasmonate (Takeda et al., 1999). Similar *cis*-acting elements have also been found in *Tnt1* (Mhiri et al., 1997).

These regulatory effects come from intrinsic structural features of different TE superfamilies. For example, LTRs have their own *cis*-regulatory sequences and RNA Pol II promoters at both ends. The 5' LTRs of plant retrotransposons contain major *cis*-acting sequences that are involved in their transcriptional activity. For example, in tobacco, LTR sequences located upstream of the TATA box promoted up-regulation to a heterologous promoter (J. M. Casacuberta & Grandbastien, 1993). LINEs possess an internal RNA Pol II promoter located in their 5' UTR. Although MITEs do not require transcription for transposition, a subset of MITEs has been shown to contain transcription factor binding sites (TFBSs) within their sequences (Soundiramourthy & Mirouze, 2025). In *Brassica* crops, for instance, the amplification of MITE elements has contributed to the genome-wide expansion of E2F TFBSs, illustrating how non-autonomous DNA transposons can act as vehicles for the proliferation of *cis*-regulatory motifs (Hénaff et al., 2014).

More broadly, only a fraction of TEs carrying regulatory motifs appear to be stably retained and co-opted by the host genome, reflecting a selective process that favors finely tuned regulatory interactions over time (Chuong et al., 2017), as exemplified by *Renovator* retrotransposon insertion, which reactivated pathogen-responsive *R* genes (Hayashi & Yoshida, 2009). A summary of *cis*-regulatory motifs identified in plant TEs from the literature is presented in Table 1.

4.2 | TEs and their regulatory effects on RNAs

TEs and non-coding RNAs (ncRNAs) have intricate relationships, such as TE domestication into microRNAs (miRNAs) (Y. Li et al., 2011; Priyapongsa & Jordan, 2008) and lncRNAs

TABLE 1 *Cis*-regulatory motifs detected in plant transposable elements.

Transposable element name/family	<i>Cis</i> -regulatory motifs	Plant species	Authors
LTR/Tto1	TGGTAGGTGAGAT	Tobacco (<i>Nicotiana tabacum</i> L.)	(Takeda et al., 1999)
MITE/mPing	ACGTATERD1, ARR1AT, CGACGOSAMY3, GARE1OSREP1, GATABOX, GTGANTG10, HEXMOTIFTAH3H4, INRNTPSADB, WBOXATNPR1, among others	Rice (<i>Oryza sativa</i> L.)	(Naito et al., 2009)
LTR/GREB-1	ACE, Box-4, G-Box, and LAMP-element	Cotton (<i>Gossypium barbadense</i> L.)	(Cao et al., 2015)
LTR/redTE	DREB/CBF	Apple (<i>Malus domestica</i> Suckow Borkh.)	(L. Zhang et al., 2019)
LTR/DKRE1	WRKY710S, WBOXATNPR1, Box-W1, L-box, MBS, EBOXBNNAPA, ELRECOREPCRP1, MYBCORE, W BOX, GATA-motif, and BOXLCOREDCPAL	Persimmon (<i>Diospyros kaki</i> Thunb.)	(X. Du et al., 2015)
LTR	NAC055, NAC080, MYC4 (BHLH), ILR3 (BHLH), TCP16, DRE-like, DRE-like, among others	<i>Arabidopsis thaliana</i> L. and Tomato (<i>Solanum lycopersicum</i> L.)	(Deneweth et al., 2022)
DNA transposon	AtHB5, AtHB2, AtHB7, AHL20 (AT-hook), AT3G10113 (SANT/MYB), CCA1 (SANT/MYB), AT3G11280 (SANT/MYB), HSEs binding site motif, SBP-box (zinc finger) among others	<i>Arabidopsis thaliana</i> L. and Tomato (<i>Solanum lycopersicum</i> L.)	(Deneweth et al., 2022)

originating from TEs carrying diverse regulatory functions (decoys, sponges, or scaffolds for RNA-binding proteins) (Gebrie, 2023; Johnson & Guigó, 2014; Kirov et al., 2020). Additionally, TE-derived small interfering RNAs (siRNAs) have been reported in several plant species. For example, in rice, a Dicer-like 3 homolog produced a 24-nt siRNA predominantly associated with MITEs (Cho, 2018; L. Wei et al., 2014).

Several cases in rice illustrate the complex interplay between TEs and TE-derived ncRNA in gene regulation. For instance, the TE-derived miRNA820 targets and down-regulates the *OsDRM2* gene, which is involved in silencing TEs. Examples include TEs that produced a miRNA to suppress host silencing machinery (Nosaka et al., 2012) and siRNA815, derived from an intronic MITE, that repressed the *ST1* gene via RNA-directed DNA methylation (RdDM), modulating resistance to *Xanthomonas oryzae* (H. Zhang et al., 2016). Lastly, in the study conducted by Fan et al. (2016), the lncRNA *PMSIT* was shown to produce phased siRNAs that play a key role in regulating photoperiod-sensitive male sterility, a trait critical for hybrid seed production. Interestingly, the authors also identified a 65-bp insertion within *PMSIT*, flanked by sequences similar to those encoding transposon proteins. This inserted fragment exhibited high similarity to multiple loci across the genome, suggesting a possible transposon-related origin (Fan et al., 2016).

In recent years, the role of ncRNAs has also been explored as an important part of plant responses to abiotic stresses

(Ahmed et al., 2020; Ramakrishnan et al., 2021). For example, in *Arabidopsis*, abiotic stress stimulated the production of non-polyadenylated lncRNAs, which regulated the flowering process and maturation (Csorba et al., 2014). Another study in *Brassica* crops performed a genome-wide analysis of lncRNA expression profiles under heat stress conditions. The researchers discovered 4594 putative lncRNAs and constructed co-expression networks involving differentially expressed lncRNAs, mRNAs, and miRNAs. They identified 25 highly co-expressed lncRNAs with homology to 10 heat-responsive genes. Notably, one lncRNA (TCONS_00048391) was found to act as an endogenous target mimic for bra-miR164a, a well-conserved plant miRNA, potentially influencing the expression of the *NAC1* gene, which is associated with heat tolerance (A. Wang et al., 2019).

Overall, TEs play a pivotal role in RNA-mediated regulation, shaping both the structural and functional landscapes of genomes. Thus, understanding TE influence in phenotype and stress response via ncRNA is crucial for future crop breeding purposes.

4.3 | Control over TEs: The importance of epigenetic regulation and side effects on gene expression

TE activity is tightly regulated by host epigenetic mechanisms (Figure 2d) to prevent their uncontrolled proliferation within

the genome. Many epigenetic features are associated with TEs, such as heterochromatin formation, DNA methylation, RNA interference (RNAi), and histone marks (X. Cui & Cao, 2014; Hassan et al., 2023; Hirsch & Springer, 2017). New TE insertions often trigger these epigenetic mechanisms, which can spread to nearby genes and influence their regulation. Notably, TEs are usually associated with reduced neighboring gene expression, as reviewed by Hollister and Gaut (2009).

The correlation between methylation levels and TE activity is opposite, meaning that the lower the methylation levels are, the greater the possibility for TE mobilization/reactivation. In plants, the predominant epigenetic regulator is RdDM, which functions using an RNA-induced silencing complex (RISC) to induce transcriptional gene silencing (TGS) (Galindo-González et al., 2018). The RISC depends on small RNA molecules (approximately 21–24 nucleotides), generally of two types, short interfering RNA and miRNA. siRNA is produced by the RNase III-like protein (DICER-LIKE) that functions as sequence-specific guides to silence or regulate genes, transposons, and viruses, besides modifying chromatin and genome structure. They also guide ARGONAUTE proteins to trigger degradation of target mRNAs (X. Cui & Cao, 2014; Xie et al., 2004). Similarly, miRNAs are generated from non-coding transcripts with self-complementary regions that form hairpin structures. These primary miRNAs are transcribed by RNA Pol II and processed by DICER-LIKE 1 into mature miRNAs, which are also incorporated into AGO-containing RISCs to direct post-TGS (Y. Li et al., 2011; Piriyaopongsa & Jordan, 2008). When studying the effects of TEs in the pollen vegetative nucleus in *A. thaliana*, TE expression coincided with down-regulation of the heterochromatin remodeler DDM1 and of many TE siRNAs (Miura et al., 2001; R. Keith Slotkin et al., 2009), which showed that the reducing methylation levels could lead to TE reactivation.

Mobile elements in plants are methylated in CG, CHG, and CHH (where H can be A, C, or T) contexts (West et al., 2014), in which CG and CHG methylation (maintained by MET1 and CMT3) silence longer, more established TEs (Saze & Kakutani, 2011; Zemach et al., 2013). West et al. (2014) compared transposon methylation in maize to *A. thaliana* and found out that most maize transposons, located in intronic regions, were highly methylated at CG and CHG sites and were enriched for histone modification H3K9me2, a pattern similar to that observed in Arabidopsis. Another example comes from two *Vitis vinifera* varieties, in which transposons and gene flanking regions exhibited high levels of DNA methylation, particularly at CHH sites (T. L. Wei et al., 2025).

Another study in Arabidopsis investigated the effects of TE epigenetic silencing and found that DNA methylation negatively affected expression of nearby genes. Moreover, purifying selection acted predominantly in methylated TEs near genes, highlighting a trade-off between restricting TE proliferation but at the cost of affecting the expression of

neighboring genes (Hollister & Gaut, 2009). Reduction in expression of nearby genes through epigenetic silencing is also reported in wheat (Hassan et al., 2023). There are reports of important agricultural traits being influenced by TE epigenetics. For example, in oil palm (*Elaeis guineensis* Jacq.), reduced methylation levels of an intronic LINE element during tissue culture lead to mantling—a somaclonal variation that results in defective fruit development and drastic yield reduction (Ong-Abdullah et al., 2015). Different plant species may have evolved distinct strategies for controlling TEs, as observed in clonally propagated duckweed (*Spirodela polyrrhiza* (L.) Schleid.). The duckweed exhibited low levels of DNA methylation and very low expression of RdDM components. Its transcriptionally silenced TEs were marked by H3K9me1 and H3K27me1, which differs from the typical silencing patterns observed in most angiosperms (Dombey et al., 2025), suggesting that diverse silencing mechanisms exist in plants.

In summary, the epigenetic regulation of TEs plays a dual role: it safeguards genome integrity by repressing potentially harmful TE activity while also promoting genetic diversity by influencing the expression of neighboring genes.

5 | OMICS ANALYSES FOR TE UNDERSTANDING: APPROACHES AND INSIGHTS

The integration of multiple omics analyses has been essential for identifying TE insertion and absence patterns, analyzing their transcriptional regulation, and assessing the functional impacts of these sequences on genomes, including their role in stress responses (Papolu et al., 2021). In this context, genomics, transcriptomics, and epigenomics (Figure 3) have become essential for elucidating the complexity of the plant genome and its evolutionary and functional implications. Genomic approaches help map TEs' location and investigate their impact in genomes; transcriptomic approaches focus on understanding TE activation and expression patterns; and lastly, epigenomics explores TE regulation mainly by DNA methylation (Figure 3), which helps to understand genome plasticity and its consequences on plant adaptation and evolution.

Research conducted before the rise of omics approaches focused on identifying and characterizing new TE families in plants. These studies largely relied on first-generation sequencing technologies, which were low-throughput and lacked automation (Eren et al., 2022). Among these early studies, Leeton and Smyth (1993) employed subcloning of relevant fragments using plasmids and Sanger sequencing to investigate genetic features of *Lilium speciosum* Thunb. The researchers identified scattered, repetitive regions exhibiting characteristics of non-LTR retrotransposons, classified as

TRANSPOSABLE ELEMENTS MULTI-OMICS APPROACHES

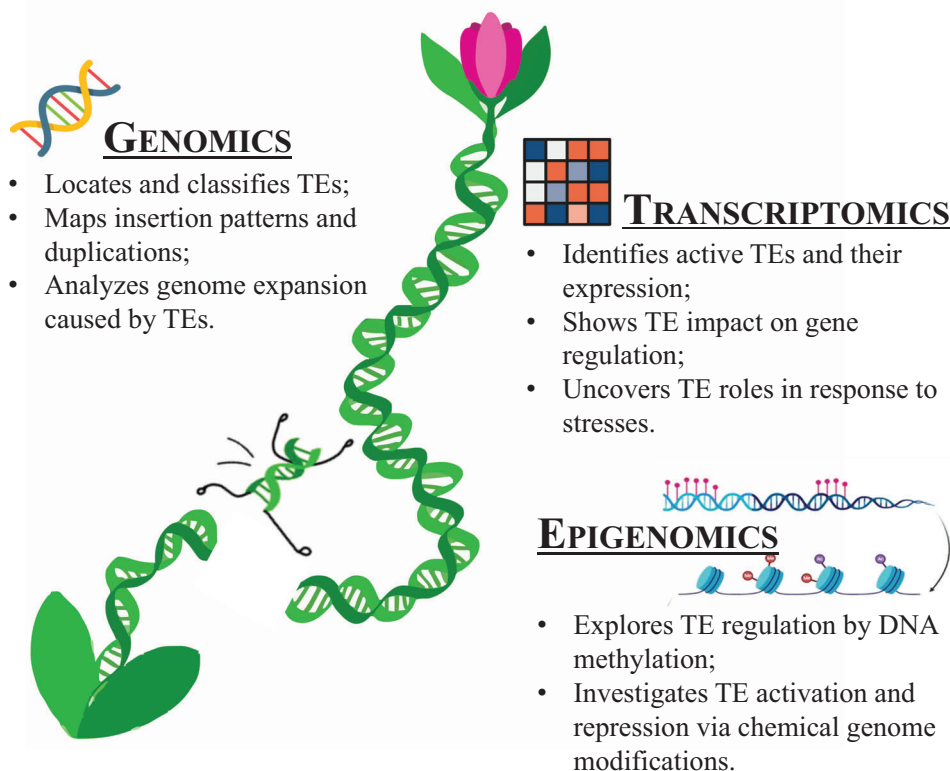


FIGURE 3 Multi-omics approaches applied in transposable elements studies.

LINE-like, suggesting the abundance of this region in the *L. speciosum* genome. Similarly, Hu et al. (1995) performed cloning and Sanger sequencing that was able to identify a new LTR retrotransposon of the Ty3/Gypsy type named *Zeon1* in maize.

Since the genome sequencing of *A. thaliana* (The Arabidopsis Genome Initiative, 2000), additional omics approaches, particularly genomics, began to expand, enabling a global understanding of TEs in plant species. The first findings combining genomics and TEs came from the project mentioned, which reported that TEs comprised 10% of the analyzed genome, with 2109 classified as class I transposons and 2203 as Class II. Identified TEs included Copia and Gypsy-type LTRs, LINEs, short interspersed nuclear elements, hobo/Activator/Tam3 (hAT), CACTA, and MITEs. Similarly, with genomic data made available by the International Rice Genome Sequencing Project (Eckardt, 2000), it was acknowledged that TEs made up 19.9% of the genome, with a greater number of Class II than Class I elements with MITEs being the most representative element (71.6%) (Turcotte et al., 2001).

The following years brought technologies such as microarrays, and with that, research using transcriptomic approaches gained prominence. Hudson et al. (2003) identified that

proteins FHY3 and FAR1, transcription factors in the phytochrome-A (phyA) signaling pathway, shared homology with DNA transposons from the MULE family, as observed when comparing the genes to known transposase domains. Their study suggested that ancient transposases were co-opted by the host genome to function in the transcriptional regulation of phyA in *A. thaliana*. Similarly, Jiao and Deng (2007) analyzed the expression profiles of genes whose ORFs contained characteristics of TEs. In their study, genes encoding TE-protein domains (i.e., domains that encode reverse transcriptases for Class I and transposases for Class II elements) were classified as TE-related genes. The expression of these genes was examined across different developmental stages of *Oryza sativa*. The authors found that TE-related genes generally exhibited lower transcriptional activity compared to non-TE-related genes, with the MULE and CACTA superfamilies showing the highest expression among the TE-related groups.

Afterward, whole-genome sequencing of several plant species was accelerated due to increased processing speed and reduced costs associated with NGS technologies (Satam et al., 2023; Shendure et al., 2017). This revolutionized TE research by enabling detailed studies of TE distribution and comparative genomics with an emphasis on these

elements. For instance, Qin et al. (2014), when comparing the genomes of a domesticated pepper species (*Capsicum* spp.) and its wild counterpart, reported significant genome expansion in the domesticated species due to LTR proliferation. Similarly, González and Deyholos (2012), after the nuclear genome sequencing of flax (*Linum usitatissimum* L.) (Z. Wang et al., 2012), sought to identify and characterize TEs in this species. They found that LTR retrotransposons Gypsy and Copia accounted for 69% of identified TEs, followed by non-LTR retrotransposons of the L1 group (11.77%) and DNA transposons of the Mutator superfamily (9%).

A notoriously challenging task is TE annotation due to their repetitive nature and abundance in the genomes (Bourque et al., 2018; Rodríguez & Makiłowski, 2022; Sahebi et al., 2018). Previously, TE dynamics were largely inferred from single-reference genomes often assembled from short reads, and this methodology is strongly influenced by sequencing and genome features, meaning that characteristics such as read length, coverage, and repeat content can negatively impact an accurate annotation (Daigle et al., 2025). Another representative challenge for early annotation is that different software can produce markedly different estimates of TE abundance and diversity (Rodríguez & Makiłowski, 2022).

Recent advances in genome assembly contiguity and accuracy, enabled by long-read sequencing technologies (e.g., PacBio and Oxford Nanopore), together with pan-genomic frameworks, are substantially improving our capacity to investigate TE dynamics, enabling the detection of both young and ancient elements, nested insertions, and lineage-specific variants. In this context, specialized annotation tools for this new scenario are emerging. For example, TrEMOLO is a tool designed to accurately estimate TEs allele frequencies using long-read sequencing data to reliably detect full-length TE insertions and precise breakpoints in population level, overcoming limitations inherent to short-read-based methods (Mohamed et al., 2023). Additionally, the development of pan-genome oriented pipelines, such as panEDTA in EDTA (Ou et al., 2024) that is able to reveal the extensive variation in TE content and insertion polymorphisms across individuals and populations, providing unprecedented resolution for studying TE activity, age distributions, and genome–phenotype associations.

The advancement of omics has contributed to our understanding of TEs, providing a broader view of their impact on phenotypic traits, opening new perspectives for plant breeding (Hassan et al., 2023). The application of multi-omics approaches enables the identification and analysis of genomic insertion patterns and TE regulation, as well as the evaluation of their functional impacts on plant genomes. Such studies have demonstrated the role of TEs in environmental stress responses, contributing to plant genomic plasticity. TE-mediated gene regulation constitutes a crucial mechanism that allows plants to adapt more

efficiently to diverse environmental conditions (Deneweth et al., 2022).

Over the years, multi-omics approaches have made it possible to understand very complex interactions in plant studies. For example, the study by Ito et al. (2016) uncovered how the TE *ONSEN* becomes activated by heat stress and causes heritable physiological changes in plants. Through genomic analysis, the researchers identified new *ONSEN* insertions, notably in ABA-responsive genes like *ABI4* and *ABI5*, linking transposition to altered hormone sensitivity. Transcriptomic analyses, including microarrays and quantitative polymerase chain reaction, showed that these insertions led to down-regulation of the target genes, helping explain the observed abscisic acid insensitivity during germination. Lastly, epigenomic profiling revealed that *ONSEN* activation is normally suppressed by RdDM but becomes active under stress in RdDM-deficient backgrounds (Ito et al., 2016). Another multi-omics study investigated the “apricot” color in raspberries (*Rubus idaeus* L.) of the Varnes cultivar. This analysis revealed low anthocyanin production in these fruits. This trait is caused by a TE similar to CACTA in the anthocyanidin synthase gene *Ans-I*, which affects anthocyanin production. Genomics played a key role by enabling whole-genome sequencing, which allowed the identification of the specific mutation responsible for the coloration. Additionally, transcriptomics enabled the analysis of gene expression patterns related to anthocyanin biosynthesis. Finally, metabolomics revealed that these fruits have a lower concentration and diversity of anthocyanins compared to red raspberries. This research highlights how TEs can shape important phenotypic traits in plants and how the integration of omics is essential to deciphering the complex genetic interactions underlying phenotype formation (Sargent et al., 2025).

Recently, research has revealed that TEs also play a crucial role in the evolution of C4 photosynthesis in species of the genus *Flaveria*. This was achieved using omics approaches through chromosome-level genome assemblies in five species. TEs significantly contributed to genome expansion during the evolutionary transition from C3 to C4; for example, genes like *PEPC1* were duplicated through TE-mediated retrotranspositions, leading to functional diversification of these genes and facilitating adaptation to C4 photosynthesis. These duplications resulted in gene copies with higher transcript abundance and adaptations to the energy demands of the new metabolic pathway. These findings underscore the importance of TEs in the evolution of a strategic plant trait and highlight the utility of omics approaches in understanding the complex mechanisms of genetic regulation and evolution (Lyu et al., 2025).

Omics-based approaches revealed that TEs play a significant role in the evolution of plant genomes, influencing key traits, genetic diversity, and plant adaptation. Research in plants has deepened our understanding of the forms,

origins, and impacts of TE activation. However, the genetic and epigenetic influence of TEs on host genomes remains an area requiring further investigation, as their presence can affect genetic recombination in the regions where they are inserted (see Section 4). Recent advances in DNA sequencing and associated technologies have transformed transposon research, paving the way for crop engineering. These innovations enable a more comprehensive exploration of the mechanisms by which TEs influence genome evolution and function, offering new perspectives for plant breeding and agricultural biotechnology.

6 | PLANT MOBILOME AND ITS IMPACT ON CROP BREEDING

Mobilome refers to the entire set of TEs present in a genome. It represents a significant portion of most eukaryotes, including many agriculturally important plants, such as maize (Schnable et al., 2009), rice (Akakpo et al., 2020), tomato (Domínguez et al., 2020), bread wheat (T. Wicker et al., 2018), and some grasses (Feschotte et al., 2002), among others. Even though transposon activity can lead to genome instability, disrupting essential genes or causing epigenetic silencing (R. K. Slotkin & Martienssen, 2007), the plant mobilome may potentially create new genetic variations, influence gene expression, and contribute to genome plasticity under environmental stresses (Lisch, 2013), which can be harnessed for crop breeding purposes. TEs can create novel alleles and regulatory elements that may enhance important agronomic traits such as drought tolerance (Mao et al., 2015), stress adaptation (Naito et al., 2009), and disease resistance (Y. H. Wang & Warren, 2010) and, consequently, improve crop yield and quality.

In recent years, the understanding of TEs effect on genetic variation has advanced significantly, particularly regarding their contribution to crop adaptation and improvement through gene regulation (Gill et al., 2021). Several studies have demonstrated how the mobilome influences the expression of agronomically important genes, resulting in phenotypic diversity relevant to breeding. For instance, J. Liu et al. (2020) identified a 4.8 kb copia-like LTR inserted in the promoter region of the *BnSHPI.A9* gene in *Brassica napus*. This insertion caused hypermethylation of the promoter, silencing gene expression and increasing resistance to pod shattering—a highly desirable trait that minimizes seed loss during harvest. Similarly, Mao et al. (2015) reported that a MITE insertion in the promoter of the *ZmNAC111* gene in maize repressed its expression via RdDM, significantly enhancing drought tolerance. In tomato, TE insertions have also been linked to important agronomic traits, such as fruit color and leaf morphology. A RIDER insertion in the *PSY1* gene was associated with fruit color variation, while a COPIA

insertion in the *BLI2* gene influenced leaf shape (Domínguez et al., 2020).

Beyond individual gene studies, recent research has incorporated transposon insertion polymorphisms (TIPs) into genome-wide association studies (GWAS), revealing novel trait-associated variants that are not captured by traditional single-nucleotide polymorphism (SNP)-based approaches. For example, in rice, LTR-retrotransposon insertions correlated with grain width variation, uncovering genetic variation previously overlooked in SNP-only analysis (Akakpo et al., 2020). In addition to enhancing trait discovery through GWAS, TEs have also been explored as molecular markers, as they can capture genetic variability more comprehensively than traditional markers such as simple sequence repeats or SNPs (Venkatesh & Nandini, 2020). Recently, researchers developed a pipeline to detect TE insertions (TEmarker) and applied this to GWAS data from 176 *Oryza sativa* subsp. *japonica* genotypes to explore associations between TE variations and specific agronomic traits. The study suggests that TE markers can capture genetic associations that might be missed by SNPs alone. It highlights the association of the gene *LOC_Os11g08410* with variations in plant height and panicle length (Yan et al., 2022). For instance, MITEs are considered prominent for molecular marker usage given their short sequence size (~100–800 bp), high frequency of insertion polymorphism, and preferential insertion in genic regions. Therefore, they could help in the identification of true hybrids for trait mapping (Venkatesh & Nandini, 2020).

Another promising application of the plant mobilome for breeding purposes is its potential to induce transgene-free mutations, enabling crop improvement while bypassing GMO (genetically modified organism) regulations (Kirov, 2023). To achieve this, Kirov (2023) reviewed several artificial strategies to cause TE reactivation, including the TEGenesis method—which combines zebularine (an inhibitor of DNA methyltransferases) and α -amanitin (an RNA Pol II inhibitor) to trigger TE activation (Thieme et al., 2017), as well as stress-mediated TE transposition and CRISPRi-based knockdown of genes involved in the RdDM pathway.

TEs applied to the CRISPR/Cas9 system will be reviewed briefly in Section 9. Overall, the plant mobilome represents a versatile genomic component with significant implications for crop improvement with the potential to contribute to more resilient, productive, and sustainable agricultural systems worldwide.

7 | TEs INFLUENCING SPECIFIC GENE/TRAITS IN PLANTS

Recent studies have shown that insertions of TEs can influence important phenotypic traits. In this section, examples are organized according to phenotypic effects, beginning

with TE-mediated changes in pigmentation and secondary metabolism. The work by Butelli et al. (2012) reported that the insertion of a Copia-like retrotransposon into the promoter of the *Ruby* gene in blood oranges (*Citrus sinensis* (L.) Osbeck) induces its expression in a cold-dependent manner, leading to the accumulation of anthocyanins in the fruit. In strawberry (*Fragaria vesca* L.), the insertion of a Gypsy retrotransposon into the *FvMYB10* gene resulted in the inhibition of the anthocyanin biosynthetic pathway, leading to the development of white fruits (Yu et al., 2024). Chopra et al. (1999) studied the molecular characterization of a variable pigmentation phenotype in sorghum (*Sorghum bicolor* (L.) Moench). According to the authors, the *Y* gene, responsible for producing red pigments in the grain pericarp, contains the active TE Candystripe1 (Cs1), which belongs to the CACTA superfamily. This element, with 23,018 bp and delimited by 20 bp terminal inverted repeats, has been associated with the y-candystripe (y-cs) phenotype, characterized by a variegated pigmentation pattern. Excision of this Cs1 can revert the phenotype to red pericarp (Chopra et al., 1999). Lastly, in apple tree the insertion of an LTR-type retrotransposon called *redTE* near the *MdMYB1* gene was a determining factor in regulating fruit color. While variants with the *redTE* insertion exhibit red fruit, the absence of these TEs is associated with yellow coloration, highlighting the direct phenotypic impact of these elements (Yu et al., 2024).

Regarding literature about TEs and fruit development and size, in grapevine, the insertion of a TE in the promoter region of the *VvPI* gene results in its ectopic expression during early fruit development, inhibiting the differentiation of mesocarp cells and preventing the formation of fleshy tissue (Fernandez et al., 2013). In apple trees, the presence of a TE in the terminal region of a pri-microRNA (miRNA172p) was associated with increased fruit size by modulating the expression of *APETALA2* family genes and promoting changes in the pattern of cell division and expansion (Yao et al., 2015). Lastly, the insertion of LTR retrotransposon *Rider* mediated an unusual gene duplication event that relocated *SUN* gene in tomato and resulted in its elevated expression. This upregulation led to the characteristic elongated fruit phenotype (Xiao et al., 2008).

When under adverse conditions, such as abiotic or biotic stress, TEs play essential roles in reprogramming gene expression. In rice, under phosphorus deficiency, TEs associated with the Pup1 quantitative trait locus were activated, leading to the modulation of genes related to phosphorus homeostasis, contributing to the efficient use of this nutrient in tolerant genotypes (Kaur et al., 2024; Seem et al., 2024). This example demonstrates how TEs can serve as adaptive mediators in resource-limited scenarios. Similarly, in *A. thaliana*, the insertion of TE into the intron of the *FLOWERING LOCUS C (FLC)* gene contributed to early flowering,

adapting the plant to environments that require shorter vegetative cycles (Sahebi et al., 2018). More on TEs and their role in plant adaptation will be addressed in the next section (Section 8).

Thus, the interaction between TEs and specific genes has profound implications for genomic evolution and phenotypic adaptation, positioning these elements as essential mediators of genetic and regulatory variability (Table 2). Therefore, continued research into the mechanisms of action of TEs paves the way for applications in genetic improvement, especially in the development of resilient and productive plant varieties in the face of climate change and the growing demand for sustainable resources.

8 | TEs CAN BE MAJOR PLAYERS AGAINST CLIMATE CHANGE

Climate change poses an escalating threat to global food security. It is characterized by extreme temperatures, prolonged droughts, flooding, and soil salinization. These environmental stressors significantly impact crop productivity and quality, presenting a major challenge for agriculture worldwide and generating significant socioeconomic consequences (Henry, 2020; Verma et al., 2025). Notably, key crops such as wheat, maize, rice, and soybeans (*Glycine max* (L.) Merr.)—cornerstones of the global food supply—already face yield reductions in several regions due to heat stress and water scarcity driven by global warming (Lobell et al., 2011; Ray et al., 2019). Moreover, fluctuations in temperature can facilitate the emergence and spread of plant pathogens by altering pathogen-host dynamics, promoting pathogen evolution, and affecting vector physiology.

Given these challenges, the development of innovative strategies to enhance crop resilience has become urgent. Among the emerging tools, TEs have garnered attention for their potential role in plant adaptation to adverse environmental conditions. The ubiquity and abundance of TEs in eukaryotic genomes underscore their evolutionary importance, particularly in plant species where certain elements are activated or regulated in response to stress stimuli (Feschotte & Pritham, 2007; Lisch, 2013). Under environmental stress—such as drought, salinity, or extreme temperatures—TEs can become mobilized, generating genetic variability through gene expression modulation, structural mutations, or the creation of novel regulatory networks. TE mobilization affects transcriptional activity of the surrounding genes, which can result in an adaptive response to the above-mentioned stress conditions (M. A. Grandbastien, 2015; Lanciano & Mirouze, 2018). For example, in tobacco, the Tnt1 element was found to be induced during biotic and abiotic stresses (M. A. Grandbastien et al., 2005). These findings support the idea that

TABLE 2 A selection of genes influenced by transposable elements in different crop species, including their type, phenotypic effect, and literature source.

Gene	Species	Transposon	Effect	Reference
<i>Ruby</i>	Blood Orange	Copia-like Retrotransposon	Cold-dependent anthocyanin accumulation	Butelli et al. (2012)
<i>VvTFL1A</i>	Grapevine	Hatvine1-rrm (hAT)	Inflorescence and fruit cluster development	Fernandez et al. (2010)
<i>Y</i>	Sorghum	Candystripe1 (CACTA)	Variegated pigmentation	Chopra et al. (1999)
<i>MdMYB1</i>	Apple	redTE (LTR Retrotransposon)	Red fruit coloration	L. Zhang et al. (2019)
<i>FvMYB10</i>	Strawberry	Gypsy Retrotransposon	White fruit phenotype	Castillejo et al. (2020)
<i>SUN</i>	Tomato	Rider (LTR Retrotransposon)	Elongated fruit shape	Xiao et al. (2008)
<i>RoKSN</i>	Rose and strawberry	Copia (Retrotransposon)	Continuous blooming	Iwata et al. (2012)
<i>CmWIP1</i>	Melon (<i>Cucumis melon</i> L.)	Gyno-hAT (hAT)	Sex determination	Martin et al. (2009)

TE-mediated genome plasticity could provide a reservoir for rapid environmental adaptation.

The contribution of TEs to crop resilience is further evidenced by their involvement in stress-responsive gene regulation (Finatto et al., 2015; Makarevitch et al., 2015; Negi et al., 2016; Sahebi et al., 2018). In rice, for example, the DNA transposon *mPing* is activated in response to cold and salt stress (Naito et al., 2009). Studies reinforce that the mutational pressure exerted by TEs like *mPing*, which preferentially insert into regulatory regions, can promote the rewiring of gene transcriptional networks, as observed in rice under cold stress (Naito et al., 2009; Yasuda et al., 2013). In maize, TE influence in gene expression was evaluated against abiotic stresses (heat, cold, high salt, and high UV incidence). For each stress condition analyzed, the authors identified four to nine TE families associated with gene expression induction. These included the terminal inverted repeat, LTR Gypsy-like, LTR Copia-like, and LINE superfamilies, as well as some elements not classified into known families (unknown). The study suggested that TEs located near genes contribute to stress responses (except UV response), as evidenced by the identification of the DREB/CBF consensus sequence—known stress-responsive transcription factors—in most TEs associated with the expression of nearby genes.

In tomato, genomic studies have revealed that the retrotransposon *Rider* is activated under drought conditions via ABA signaling. Its terminal regions harbor *cis*-regulatory elements associated with dehydration and ABA response pathways (Benoit et al., 2019). Similar observations have been made for TEs such as *Bare1* and *Fare1*, which also contain ABA-responsive elements and are implicated in drought stress responses (P. He et al., 2012; Vicent et al., 2001).

Beyond causing direct genetic alterations, TEs also influence epigenetic regulation, allowing plants to “remember” past stress exposures and prime subsequent generations

for enhanced stress tolerance (Mirouze & Paszkowski, 2011). This phenomenon, known as transgenerational epigenetic inheritance (Paszkowski & Grossniklaus, 2011), may reduce the time between environmental change and adaptive response—an essential feature in rapidly changing ecosystems. Moreover, TE-induced epigenetic variation may also complement conventional breeding efforts by introducing stable, non-Mendelian traits adapted to unpredictable environments.

Therefore, the plant mobilome can be a major player against climate change as it can contribute to plant genetic variability, gene expression modulation, and the development of stress-responsive regulatory networks. These features are “hidden treasures” that eventually can be explored for enhancing crop resilience.

9 | POTENTIAL OF TEs IN PLANT BREEDING AND BIOTECHNOLOGY

Although TEs constitute a significant fraction of the genomes in numerous economically important crops (Lisch, 2013), their application in plant breeding remains largely underexploited. Nevertheless, in recent years, a growing array of technologies has been deployed to unlock their latent biotechnological potential.

One major application is insertional mutagenesis, where TEs act as natural mutagens that generate phenotypic diversity (Hassan et al., 2023). For example, the *Tnt1* retrotransposon in *Medicago truncatula* Gaertn. has enabled the creation of mutant libraries that reveal genes crucial for symbiosis and stress responses (Pislariu et al., 2012; Tadege & Mysore, 2011). Similarly, the rice *Tos17* retrotransposon has helped uncover genes linked to disease resistance and grain yield (Jun et al., 2019; Sabot, 2014). These actions accelerate functional genomics by quickly linking genotypes to traits and

streamlining the identification of crop-improvement targets (Jun et al., 2019; Sabot, 2014).

Beyond mutagenesis, TEs serve as molecular markers for gene cloning (Dubin et al., 2018; Hassan et al., 2023). The maize *Ac/Ds* system (C. Du et al., 2011), for instance, has been instrumental in tagging other genes involved in flavonoid biosynthesis and kernel development (C. Du et al., 2011; Jun et al., 2019; Sabot, 2014), while the barley (*Hordeum vulgare* L.) *BARE-1* retrotransposon has been used to map stress-responsive loci to facilitate marker-assisted selection (Ito et al., 2016; Negi et al., 2016).

Recent advancements in genome engineering have expanded TE utility even further (Simpson & Chuong, 2023). The CRISPR-Cas9 system, which evolved from bacterial defenses against invading genetic elements (such as bacteriophages) (Simpson & Chuong, 2023), now underpins precision genome editing in crops (Lisch, 2013). Engineered transposons (e.g., modified PiggyBac) enable scarless gene insertion in soybean and tomato (Nishizawa-Yokoi & Toki, 2023), allowing for trait stacking (e.g., combining phytopathogens resistance with drought tolerance) without linkage drag (Negi et al., 2016; Simpson & Chuong, 2023). In addition, recent work on transposase-assisted target-site integration has shown that combining rice Pong transposase protein with the Cas9 or Cas12a resulted in a sequence-specific targeted insertion of enhancer elements, an ORF, and a gene expression cassette into the genome of the model plant *Arabidopsis*, and it was later on applied in soybean, further expanding the utility of TE-based engineering systems (P. Liu et al., 2024). Moreover, TEs play a pivotal role in modulating epigenetic regulation, particularly through their influence on DNA methylation and histone modifications (Mencia et al., 2024). For example, TE insertions proximal to stress-responsive genes can fine-tune their expression under adverse environmental conditions (Ito et al., 2016; Negi et al., 2016). In rice, methylation of the *OsCOP1* retrotransposon has been implicated in the modulation of flowering time—a key adaptive trait in the context of climate change (Kim et al., 2023; Vitte et al., 2007). Additionally, stress-induced changes in DNA methylation dynamically regulate retrotransposon activity and the expression of rice flowering-related genes, enabling rapid environmental adaptation via modulation of developmental timing (Ramakrishnan et al., 2021; Yin et al., 2024). By harnessing such mechanisms, breeders can develop epi-lines with stable, heritable stress tolerance (Gupta & Salgotra, 2022), thereby opening new frontiers for engineering climate-resilient crops (Gupta & Salgotra, 2022; Varotto et al., 2020). Importantly, TE-mediated epigenetic modifications—such as DNA methylation—can induce heritable phenotypic variation without altering the underlying DNA sequence (Gupta & Salgotra, 2022; Mencia et al., 2024; Varotto et al., 2020). Leveraging this layer of variation, breeders can exploit TE-induced epigenetic plasticity as a

valuable reservoir for enhancing crop performance under environmental stress (Dubin et al., 2018; Hassan et al., 2023; Lisch, 2013; Yin et al., 2024).

Genetic recombination of TEs is also instrumental considering their biotechnological applications, thereby aiding the development of hybrid crops (Dubin et al., 2018; Hassan et al., 2023; Lisch, 2013). Some TEs, like the *Veju* retrotransposon of wheat, induce double-stranded breaks that boost recombination in genomic regions typically resistant to crossover (Sabot et al., 2005), thus facilitating the introgression of beneficial genes (Dubin et al., 2018; Gupta & Salgotra, 2022; Sabot et al., 2005). In hybrids, TE activity may generate novel allelic combinations that enhance yield and robustness (Groza et al., 2024). Notable examples include natural TE insertions at the wheat *Vrn-A1* locus, which regulate vernalization and enable early-maturing cultivars (Royo et al., 2020), and also the rice *Sub1A* gene originating from a TE-mediated duplication that confers submergence tolerance to protect yields in flood-prone regions (Fukao et al., 2011; Xu et al., 2006).

TEs have become essential for genetic mapping and diversity analysis due to their repetitive nature and widespread distribution (Grzebelus, 2018). Retrotransposon-based markers, such as inter-retrotransposon amplified polymorphism and retrotransposon-microsatellite amplified polymorphism, are widely used to assess genetic diversity in crops like barley (Cheraghi et al., 2018; Pandotra et al., 2015), rice (Cheraghi et al., 2018), and maize (C. Du et al., 2011; Garcia et al., 2017). For example, the barley *BARE-1* retrotransposon has been used to trace evolutionary relationships and identify stress-tolerant wild relatives (Jääskeläinen et al., 2013). In turn, sequence-specific amplification polymorphism markers derived from rice *Tos17* enabled high-resolution genotyping for selecting elite breeding lines (Sha et al., 2005; R. Wang et al., 2015). These markers offer cost-effective, high-throughput methods for tracking desirable alleles in breeding programs (Jääskeläinen et al., 2013; Sha et al., 2005).

TEs also drive genetic variability by inducing insertions, deletions, and chromosomal rearrangements that can create novel alleles (Dubin et al., 2018; Hassan et al., 2023; Lisch, 2013). Their activity may alter gene expression, establish new regulatory networks, or even produce chimeric genes (Hassan et al., 2023). For instance, TE insertions in the promoter of the stress-responsive *DREB1A* gene in *Arabidopsis* enhance drought tolerance by upregulating stress pathways (Kidokoro et al., 2020), whereas the maize Hopscotch retrotransposon inserted upstream of *tb1* suppresses branching (Dong et al., 2017; Studer et al., 2011).

Recent efforts in genetic improvement have focused on using TEs to develop stress-tolerant, high-yielding cultivars (Fukao et al., 2011; R. Wang et al., 2015; Xu et al., 2006). In wheat, chromosome engineering-induced homoeologous recombination using TE-related technologies is widely used to reduce linkage drag during the introgression of rust

resistance genes from wild relatives into elite varieties, retaining only desirable chromosomal segments (Bariah et al., 2020; Y. Zhang et al., 2021; T. Zhao & Schranz, 2017). In maize, TIPs have been related to some retrotransposons improving root architecture and nitrogen-use efficiency (Schneider et al., 2022). Climate resilience remains a priority; for example, the TE-derived *Sub1A* locus in rice has been introgressed into mega-varieties like Swarna to confer submergence tolerance (Fukao et al., 2011; Xu et al., 2006).

Despite these advantages, TE usage is not without risks. Uncontrolled TE mobilization can destabilize the genome by disrupting essential genes or triggering harmful rearrangements (Bourque et al., 2018). Mitigation strategies include conditional activation via inducible promoters (Grzebelus, 2018), CRISPR-guided precision editing (Simpson & Chuong, 2023), and post-integration silencing through RNAi (Cornec & Poirier, 2023). Looking forward, novel research initiatives are exploring how reactivating TEs in ancestral or wild cereal varieties can reintroduce beneficial traits lost during domestication (X. Li et al., 2017), while machine learning models that predict TE insertion hotspots could optimize trait pyramiding for multi-stress-resistant crops (Panta et al., 2021; J. Y. Wang et al., 2025; Wellinger & Aguilar-Ruiz, 2022). Overall, TEs have evolved from genomic curiosities to indispensable tools in plant breeding (Hassan et al., 2023). Their ability to generate diversity (Gupta & Salgotra, 2022), regulate gene expression (Cornec & Poirier, 2023), and reshape genomes places TEs at the forefront of efforts to develop climate-resilient (Varotto et al., 2020) and nutrient-rich crops (Huang et al., 2025). As TE biology becomes increasingly integrated with advanced biotechnologies, their full potential can be unlocked to drive sustainable agricultural innovation in the face of global environmental challenges.

10 | PERSPECTIVES ON TE-BASED TECHNOLOGIES

The interplay between TEs and plant genomes offers unprecedented opportunities for crop improvement (Hassan et al., 2023; Varotto et al., 2020). Advances in synthetic biology (Muñoz-López & García-Pérez, 2010), epigenome engineering (Gupta & Salgotra, 2022), and artificial intelligence (AI) (R. Wang et al., 2024) are positioning TEs as central tools in designing next-generation crops capable of withstanding climate extremes, nutrient limitations, and emerging pathogens.

One promising frontier is the engineering of synthetic TEs for controlled genome diversification (Alseekh et al., 2020; Dayi, 2024). In ancestral maize lines, reactivating dormant TEs can recapitulate natural domestication processes that enhanced traits such as kernel size and stalk strength (Makarevitch et al., 2015; Stitzer et al., 2021). Engineered PiggyBac

transposons (Nishizawa-Yokoi & Toki, 2023), for instance, could be modified with tissue-specific promoters to ensure precise targeting without disrupting essential genes, enabling breeders to “rewire” crop genomes without the risks associated with random mutagenesis (Nishizawa-Yokoi & Toki, 2023).

Epigenome engineering is another innovative approach (Klein & Anderson, 2022). Because TEs naturally influence DNA methylation and histone modification patterns, these properties can be harnessed to create stable, heritable epigenetic changes (Gupta & Salgotra, 2022; Klein & Anderson, 2022; Varotto et al., 2020).

Future technologies may employ CRISPR-Cas9 fused with epigenetic modifiers to target TE-rich regions and alter gene expression without changing the underlying DNA sequence (Klompe et al., 2019; Padeken et al., 2023; Tenjo-Castaño et al., 2023). For example, TE insertions with demethylating effects near stress-responsive genes could activate drought tolerance pathways in crops such as wheat or rice (Yin et al., 2024), paving the way for “epi-breeding” strategies that bypass the need for transgenic modifications (Gupta & Salgotra, 2022; Padeken et al., 2023; Varotto et al., 2020).

The integration of machine learning and AI is set to revolutionize TE applications (Panta et al., 2021; R. Wang et al., 2024; Wellinger & Aguilar-Ruiz, 2022). Predictive models trained on extensive genomic datasets could identify TE insertion hotspots (Panta et al., 2021; Wellinger & Aguilar-Ruiz, 2022), optimize trait stacking (Panta et al., 2021), and forecast the phenotypic outcomes of TE-induced mutations (Panta et al., 2021; R. Wang et al., 2024). For instance, AI algorithms might predict how retrotransposon insertions affect hybrid performance in maize by analyzing historical recombination patterns (Biryukov & Ustyantsev, 2022; Orozco-Arias et al., 2023). Additionally, deep learning tools could design synthetic TEs with enhanced mobility or targeting specificity, reducing experimental trial-and-error and expediting the development of resilient cultivars (Orozco-Arias et al., 2023; R. Wang et al., 2024).

Climate adaptation will remain a critical focus for plant diversity and resistance (Varotto et al., 2020). As global temperatures rise and weather patterns become increasingly erratic, TEs offer a natural reservoir of adaptive genetic diversity (E. Casacuberta & González, 2013; Ito, 2022; K. Zhao et al., 2022). Future breeding programs may screen wild crop relatives for active TEs associated with heat tolerance (Thieme et al., 2022) or saline adaptation (C. Zhao et al., 2020), then use CRISPR to introgress these elements into elite varieties (Simpson & Chuong, 2023; Tenjo-Castaño et al., 2023). For example, the rice *Sub1A* locus could be further optimized using base editing to enhance flood tolerance (Fukao et al., 2011). Similarly, TE-mediated duplication of carbon fixation genes in C3 plants like wheat might boost photosynthetic efficiency under elevated CO₂ conditions (H. Cui,

Targeted TE Editing (CRISPR/Prime Editing)¹

Description: Enables the insertion, removal, or targeting of TEs to specific genomic regions, allowing precise control of gene expression and genetic variability.

Challenges: Insertion specificity, pleiotropic effects, and regulatory constraints.

Impact: High – accelerates the development of adapted cultivars with reduced risk of unintended effects.

TEs as Gene Drive Vectors²

Description: Utilizes TEs to disseminate desirable traits, such as pest and stress resistance.

Challenges: Ecological risks, reversibility control, and biosafety concerns.

Impact: Potentially high but requires stringent regulation.

Epigenetic TE Regulation³

Description: Modulates TEs activity through DNA methylation and histone modifications without altering the genetic sequence.

Challenges: Stability across generations and experimental validation.

Impact: High – enables the development of resilient cultivars without transgenesis, improving regulatory and public acceptance.

TE Discovery and Functionalization⁴

Description: Uses high-throughput sequencing and machine learning to identify TEs with biotechnological applications.

Challenges: Managing large-scale datasets and the need for advanced computational tools.

Impact: Medium to long-term – may reveal new tools for genetic engineering.

TE Integration with Advanced Omics⁵

Description: Combines genomics, transcriptomics, epigenomics, and proteomics to predict TE-driven gene regulation impacts.

Challenges: Data complexity and functional validation requirements.

Impact: High – may revolutionize the understanding of TE-genome interactions.

TEs in Climate Adaptation⁶

Description: Identifies TEs associated with adaptation to environmental stresses, such as drought and salinity.

Challenges: Complexity of gene-environment interactions and difficulties in introducing these traits into elite cultivars.

Impact: High – facilitates breeding for climate resilience.

TEs in Synthetic Genome Engineering⁷

Description: Programmable TE insertion to modulate regulatory networks and enhance agronomic traits.

Challenges: Technical complexity, bioethical considerations, and the need for advanced computational modeling.

Impact: Very high but long-term – could enable the rational design of customized cultivars.

BOX 1 Perspectives of transposable elements (TE) applications in crop breeding. (1) Nishizawa-Yokoi and Toki (2023); Simpson and Chuong (2023); Yasuda et al. (2013); (2) Bourque et al. (2018); Sen et al. (2024); Alseekh et al. (2020); (3) Gupta and Salgotra (2022); Mencia et al. (2024); Padeken et al. (2023); Kim et al. (2023); Yin et al. (2024); (4) Dubin et al. (2018); Hassan et al. (2023); Huang et al. (2025); Panta et al. (2021); R. Wang et al. (2024); (5) Wellinger and Aguilar-Ruiz (2022); Orozco-Arias et al. (2023); Panta et al. (2021); R. Wang et al. (2024); (6) E. Casacuberta and González (2013); Varotto et al. (2020); Thieme et al. (2022); K. Zhao et al. (2022); (7) H. Cui (2021); Swift et al. (2024); J. Y. Wang et al. (2025); Makarevitch et al. (2015); Stitzer et al. (2021).

2021; Panda et al., 2023; Swift et al., 2024), drawing inspiration from TE-driven innovations in C4 plants (H. Cui, 2021; Swift et al., 2024).

Horizontal gene transfer mediated by TEs also holds promise (Aubin et al., 2021). Although rare in plants, some TEs facilitate interspecific DNA exchange, as observed in the transfer of pest-resistance genes among grasses (Sen et al., 2024). Synthetic biology might eventually create “bridging TEs” capable of transferring beneficial traits, such as nitrogen fixation, from legumes to cereals, reducing reliance on synthetic fertilizers (Y. Li et al., 2024; Pislariu et al., 2012; Schneider et al., 2022). While significant biological challenges remain, recent advances in xenobiology suggest that these breakthroughs are achievable (Dubin et al., 2018; Ito, 2022; Muñoz-López & García-Pérez, 2010; Tenjo-Castaño et al., 2023).

Genomic instability, especially in polyploid crops, persists (Session & Rokhsar, 2023; Vicent & Casacuberta, 2017). Potential solutions include embedding “kill switches” in synthetic TEs, such as CRISPR-targeted self-inactivation sequences or light-inducible recombinases that remove TE

after integration (Klompe et al., 2019; Simpson & Chuong, 2023; Tenjo-Castaño et al., 2023). In parallel, regulatory frameworks must evolve to address epigenetic modifications and TE-driven horizontal gene transferes, balancing biosafety with innovation (Alseekh et al., 2020; Aubin et al., 2021; Simpson & Chuong, 2023; Tenjo-Castaño et al., 2023). Ethical and ecological considerations are paramount (Alseekh et al., 2020; Grzebelus, 2018). While TEs can enhance crop resilience (Sen et al., 2024; Sha et al., 2005), their unintended spread through pollen or seed dispersal might alter ecosystems (Alseekh et al., 2020; Grzebelus, 2018; Kuhn et al., 2014). Transparent public communication about these technologies will also be essential to build trust and address misconceptions (Dubin et al., 2018; Grzebelus, 2018; Lisch, 2013).

Considering all scenarios, the future of TE technologies in plant breeding, as shown in Box 1, is promising, marked by the convergence of genomics, AI, and synthetic biology. By leveraging TEs as both tools and targets, researchers can accelerate the development of high-yielding crops that are inherently adaptable to a changing climate, ensuring sustainable food production while safeguarding biodiversity.

11 | CONCLUSIONS

TEs have emerged to be increasingly recognized as key players in plant genome evolution. TEs drive genetic variability and allow plants to evolve to cope with new environmental conditions. In this review, we integrate robust evidence showing how TEs may shape phenotypic plasticity, enhance stress tolerance, and influence the regulation of important agronomic traits. They do so through a range of mechanisms, including insertional mutagenesis, *cis*-regulatory region modifications, and epigenetic alterations.

The double nature of TEs—as both possible causes of genomic instability and robust drivers of evolutionary innovation—is illustrated in several case studies, from anthocyanin production in blood oranges to the modification of fruit development in grapevines. With the improvement in omics technologies, scientists have been able to learn more about TE behavior, including their insertion preferences, interactions with host epigenetic machinery, and environmentally induced activation patterns that enable the plant to adapt to stress.

The central argument here is that TEs are fundamental to plant adaptability, serving as reservoirs of genetic and epigenetic variation that can be exploited in crop improvement. Although TE function can be a threat to genome integrity, the combination of our understanding of TE biology with modern biotechnological methodologies—such as CRISPR-mediated regulation, epigenome editing, and marker molecules derived from TEs—preliminarily offers a road map to harness their benefit at lower risk. In fact, TE-associated traits like drought and heat tolerance have already proven beneficial in addressing climate-related challenges in agriculture.

In the coming times, the full potential of TEs will be realized by interdisciplinary efforts combining synthetic biology, machine learning, and multi-omics platforms. Research priorities in the coming times will include predictive modeling to identify TE insertion hotspots, designing synthetic TEs for targeted genome engineering, and elucidating the function of TEs in mediating plant-microbe interactions for shaping resilience. Bridging the gap between foundation TE research and emerging technologies will be essential to accelerate the breeding of climate-resilient crops and strengthen global food security in an increasingly uncertain world. Long dismissed as genetic parasites, TEs are turning out to be useful partners in the ongoing pursuit of crop improvement.

AUTHOR CONTRIBUTIONS

Flávia Layse Belém Medeiros: Writing—original draft; writing—review and editing. **José Ribamar Costa Ferreira-Neto:** Writing—original draft; writing—review and editing. **Jarbson Henrique Oliveira Silva:** Writing—original draft. **Cinthia Carla Claudino Grangeiro Nunes:** Writing—

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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