**Transposable Elements in Plant Genomics: Drivers of Evolution, Adaptation, and Crop Improvement**

**Abstract**

Transposable elements (TEs) are ubiquitous genetic components that play critical roles in shaping plant genome structure, function, and evolution. Their ability to move within genomes through mechanisms such as “copy-and-paste” and “cut-and-paste” transposition contributes to genome size variation, structural diversity, and regulatory innovation. Research in the last twenty years has convincingly demonstrated that alterations in TEs may not be only the consequences of the disease, but are among those that are involved in the pathogenesis. Further knowledge that environmental stressors can affect TEs has allowed a connection to be drawn between environmental exposures, TEs, and disease development. TEs are classified into two major classes: Class I (retrotransposons) and Class II (DNA transposons), each with distinct transposition mechanisms. Retrotransposons, particularly LTR elements, are major contributors to genome expansion in species such as maize (Zea mays) and wheat (Triticum aestivum), while DNA transposons drive structural rearrangements and gene modification. TE activity is often triggered by environmental stresses, leading to increased genetic diversity and adaptability. TEs also influence gene expression by providing regulatory elements, modifying transcriptional and post-transcriptional processes, and participating in epigenetic regulation. Host genomes have evolved sophisticated mechanisms, including DNA methylation, histone modifications, and small RNA-mediated silencing, to control TE activity and maintain genome integrity. Recent advances in genome editing tools, such as transposon-based vectors and CRISPR-Cas technologies, offer novel opportunities for exploiting TEs in functional genomics and crop improvement. The use of TEs for enhancing genetic diversity, stress tolerance, and adaptability has significant implications for breeding resilient crops. Future research integrating multi-omics approaches, high-resolution sequencing, and predictive models will further elucidate TE dynamics and their contributions to plant evolution. Harnessing the potential of TEs for crop improvement will require precise manipulation of their activity and an understanding of their complex interactions with host genomes. The ongoing exploration of TEs as drivers of genome evolution and tools for biotechnology promises to enhance agricultural productivity and resilience in response to global challenges, including climate change and food security. The interplay between TEs, epigenetic mechanisms, and phytohormones highlights the intricate molecular networks that control plant stress resistance and adaptation. Understanding the role and regulatory mechanisms of TEs in response to abiotic stress could pave the way for developing stress-tolerant crops and improving agricultural sustainability in the face of global environmental challenges.

**Keywords:** *Transposable elements, Genome evolution, Retrotransposons, DNA transposons, Gene regulation, Crop improvement, Epigenetic control*

1. **Introduction**

Transposon elements (TEs) are mobile genetic elements that can make up a large portion of the plant and animal genome through movement processes. They can affect the genome by altering gene expression and influencing genome evolution. Some types of TEs can insert into a new location in the genome and disrupt or restore the function of neighboring genes or create new regulatory elements. Other TEs are more stable and remain in the same location in the genome for long periods of time (Benoit et al., 2019; Ndlovu, 2020). TEs are versatile genetic elements that play diverse and essential roles in plant genome function and evolution. TEs have the ability to influence gene regulation through epigenetic modifications and play a key role in shaping the expression patterns of neighboring genes. They also contribute to the formation of non-coding RNAs, such as long non-coding RNAs (lnc RNAs), which have been shown to be crucial regulators of various physiological processes in plants (Kaur et al., 2024; Saha et al., 2023).

**A. Transposable Elements (TEs)**

**1. Discovery of TEs (e.g., Barbara McClintock's work)**
Transposable elements (TEs), often referred to as "jumping genes," were first discovered by Barbara McClintock during her pioneering studies on maize (Zea mays) in the 1940s and 1950s. McClintock identified that certain genetic elements could change positions within the genome, causing various mutations and changes in gene expression. Her groundbreaking work was initially met with skepticism but later earned her the Nobel Prize in Physiology or Medicine in 1983, highlighting the importance of TEs as a fundamental aspect of genome biology.

**2. Definition and classification of TEs (Class I: Retrotransposons & Class II: DNA Transposons)**
Transposable elements are discrete DNA sequences capable of moving within and between genomes (Kidwell et.al., 2001). They are broadly classified into two major classes based on their transposition mechanisms:

Class I: Retrotransposons
Retrotransposons mobilize via a “copy-and-paste” mechanism involving RNA intermediates. The transposition process includes transcription of the TE into RNA, reverse transcription into cDNA, and integration back into the genome. Retrotransposons are further subdivided into Long Terminal Repeat (LTR) retrotransposons and Non-LTR retrotransposons (e.g., LINEs and SINEs).

Class II: DNA Transposons
DNA transposons utilize a “cut-and-paste” mechanism where the element is physically excised from one genomic location and inserted into another (Schmitz et.al., 2024). DNA transposons can also include rolling-circle transposons (e.g., Helitrons), which replicate through a distinct mechanism involving a single-strand DNA intermediate.

**B. Importance of TEs in Genomics**

**1. Ubiquity in plant genomes**
TEs are ubiquitous and comprise a significant portion of most eukaryotic genomes. They are particularly abundant in plant genomes, where they play a major role in genome architecture and function. Studies have shown that TEs can constitute over 85% of certain plant genomes, making them essential to understanding genome evolution and adaptation.

**2. Proportion of plant genomes constituted by TEs (e.g., maize, wheat, rice)**
The proportion of TEs varies significantly among plant species. For instance, TEs account for approximately 85% of the maize genome, primarily due to the expansion of LTR retrotransposons. In wheat, TEs make up nearly 90% of the genome, contributing substantially to its large size and complexity. Rice, a model monocot species with a smaller genome, contains approximately 35% TEs, demonstrating that even compact genomes can harbour substantial TE content.

**C. Objective of the Review**

**1. To discuss the role of TEs in genome evolution and adaptation in plants**
The primary objective of this review is to explore the multifaceted roles of TEs in plant genome evolution and adaptation (Negi et.al., 2016). TEs have been implicated in driving genome expansion, structural variation, gene regulation, and adaptation to environmental challenges. Understanding these elements provides insights into how plant genomes evolve and adapt to diverse ecological conditions.

**2. To highlight recent advances and future research directions**
This review aims to present recent discoveries concerning TE dynamics, their regulation, and their evolutionary impact on plant genomes. Emphasis is placed on technological advancements such as high-throughput sequencing and comparative genomics, which have unveiled new aspects of TE biology. Identifying future research directions will be essential for harnessing the potential of TEs in plant breeding and crop improvement (Sen et.al., 2024).

**II. Classification and Characteristics of Transposable Elements**

**A. Class I: Retrotransposons**

**1. Long Terminal Repeat (LTR) Retrotransposons**
LTR retrotransposons are one of the most abundant classes of transposable elements in plant genomes, characterized by their long terminal repeats flanking the coding regions (Lee et.al., 2014). These elements transpose via an RNA intermediate followed by reverse transcription and integration of the cDNA copy into a new genomic location. Two major families of LTR retrotransposons include Ty1-copia and Ty3-gypsy, which are prevalent across various plant genomes.

LTR retrotransposons contribute significantly to genome size variation. For instance, the maize genome is composed of approximately 75% LTR retrotransposons, with a high frequency of insertion and retention events contributing to its complex architecture. In wheat, nearly 90% of the genome consists of TEs, with LTR retrotransposons playing a predominant role in genome expansion. Their activity is often regulated by epigenetic mechanisms, such as DNA methylation, which limits their transposition and preserves genome stability.

**2. Non-LTR Retrotransposons (e.g., LINEs, SINEs)**
Non-LTR retrotransposons are retrotransposable elements that lack terminal repeats and include two major subtypes: Long Interspersed Nuclear Elements (LINEs) and Short Interspersed Nuclear Elements (SINEs). LINEs are autonomous elements capable of encoding the proteins necessary for their transposition, whereas SINEs are non-autonomous and rely on the machinery of LINEs for mobilization (Mangoni et.al., 2025). In plants, LINEs are less common than LTR retrotransposons but still play an essential role in genome evolution. In rice, non-LTR retrotransposons contribute approximately 10% of the total genome size, with various families exhibiting differential activity based on environmental conditions. SINEs, though generally rare in plants, are known to influence gene regulation by introducing regulatory elements near or within genes.

**B. Class II: DNA Transposons**

**1. Cut-and-paste transposons**
Cut-and-paste transposons are characterized by their ability to excise themselves from one genomic location and integrate into another (Halle et.al., 1997). This process is mediated by a transposase enzyme, which recognizes specific inverted terminal repeats (ITRs) flanking the transposon sequence. Prominent families of cut-and-paste transposons include Activator (Ac)/Dissociation (Ds) and Mutator (Mu) elements, which have been extensively studied in maize. While less abundant than retrotransposons, cut-and-paste DNA transposons have contributed significantly to genome plasticity in various plants. Studies have reported that they represent approximately 3% of the maize genome and about 8% of the Arabidopsis thaliana genome. Their activity can be regulated through chromatin modifications, which often silence these elements to maintain genomic integrity.

**2. Rolling-circle transposons (e.g., Helitrons)**
Rolling-circle transposons, commonly referred to as Helitrons, represent a unique class of DNA transposons that replicate via a rolling-circle mechanism rather than the classical cut-and-paste mechanism (Thomas et.al., 2015). Discovered in maize and other plants, Helitrons are capable of capturing and shuffling gene fragments, thereby contributing to gene diversification and innovation. Estimates suggest that Helitrons contribute approximately 2% of the maize genome, with evidence indicating their ability to generate new chimeric genes through exon shuffling. Unlike other DNA transposons, Helitrons lack terminal inverted repeats, instead relying on conserved sequence motifs to initiate transposition.

**C. Characteristics and Mechanisms of Transposition**

**1. Copy-and-paste vs. Cut-and-paste mechanisms**
The fundamental difference between Class I and Class II transposable elements lies in their mechanisms of transposition (Silva et.al., 2004). Retrotransposons (Class I) utilize a copy-and-paste mechanism where the original element remains at its original location, and a copy is inserted elsewhere. This process often leads to genome expansion, as seen with the proliferation of LTR retrotransposons in maize and wheat. DNA transposons (Class II), in contrast, utilize a cut-and-paste mechanism where the element is excised from one location and inserted at another. While this mechanism does not inherently increase genome size, it can promote genome rearrangement and structural diversity through non-homologous recombination and ectopic insertion events.

**2. Epigenetic regulation of transposition**
Transposable elements are tightly regulated by host genomes to prevent uncontrolled transposition, which can result in harmful mutations (Oliver et.al., 2009). Epigenetic mechanisms, including DNA methylation, histone modifications, and small RNA-mediated pathways, play critical roles in silencing TEs and restricting their mobility. Studies have demonstrated that active TEs are often associated with hypomethylated DNA regions, whereas silenced elements exhibit hypermethylation and specific histone modifications, such as H3K9me2. The regulation of TEs is particularly important in plants, where environmental stress can activate previously silenced elements, contributing to genetic diversity and potential adaptation.

**III. Transposable Elements and Genome Evolution**

**A. TE-Mediated Genome Expansion and Contraction**

**1. Contribution to genome size variation**
Transposable elements are recognized as major contributors to genome size variation across plant species (Zuccolo et.al., 2007). The proliferation of TEs can lead to significant genome expansion, a phenomenon often referred to as "genomic obesity". For example, the maize (Zea mays) genome, which is approximately 2.3 Gb in size, contains over 85% TEs, with LTR retrotransposons accounting for nearly 75% of the entire genome. Similarly, the wheat (Triticum aestivum) genome, one of the largest known among cultivated plants at approximately 17 Gb, is composed of nearly 90% TEs, predominantly LTR retrotransposons. Comparative studies have revealed a direct correlation between TE content and genome size. For instance, rice (Oryza sativa), which has a smaller genome of around 430 Mb, contains approximately 35% TEs, indicating that TE amplification is a key factor in genome size diversity. Such differences in TE content and genome size have been associated with species-specific adaptation and evolutionary processes.

**2. Mechanisms of genome expansion (e.g., TE proliferation)**
Genome expansion through TE activity primarily occurs via the "copy-and-paste" mechanism of Class I retrotransposons, which generate new copies without excising the original element (Platt et.al., 2018). The accumulation of these copies can rapidly increase genome size, as demonstrated in maize, where bursts of retrotransposon activity have been linked to significant genomic expansion over relatively short evolutionary periods. LTR retrotransposons, particularly those belonging to the Ty1-copia and Ty3-gypsy families, have been identified as the main drivers of genome expansion in various plant species. Studies on wild and domesticated wheat varieties have shown that the recent proliferation of LTR retrotransposons contributed to the formation of new subgenomes, which may enhance genetic diversity and environmental adaptation.

**3. Genome size reduction through TE elimination**
While TE proliferation promotes genome expansion, genomes can also contract through processes that eliminate TEs (Oliver et.al., 2012). These mechanisms include unequal homologous recombination, illegitimate recombination, and epigenetic silencing leading to TE degradation. In rice, illegitimate recombination has been identified as the primary mechanism for the removal of TEs, contributing to its relatively compact genome compared to other grass species. Genome size reduction can be an adaptive response to environmental pressures, suggesting that a dynamic balance between TE amplification and elimination shapes genome architecture over evolutionary time.

**B. TE-Driven Structural Variation**

**1. Chromosomal rearrangements (duplications, inversions, deletions)**
TEs are potent drivers of structural variation in plant genomes, including chromosomal rearrangements such as duplications, inversions, and deletions. These events occur primarily through non-allelic homologous recombination (NAHR) and transposase-mediated mechanisms.

Studies in maize have demonstrated that the insertion of Mutator transposons can lead to chromosomal breakage and rejoining, resulting in large-scale rearrangements that impact gene function and expression (Dooner et.al., 2013). LTR retrotransposons have also been implicated in generating inversions and segmental duplications through recombination between similar elements located on different chromosomal regions.

**2. Segmental duplications and gene duplication events**
TEs are involved in segmental duplications by promoting unequal crossing-over events. Such duplications contribute to gene copy number variation, which is a crucial mechanism for gene innovation and functional diversification. In maize, the Helitron family of rolling-circle transposons has been shown to capture gene fragments and create novel gene combinations through a process termed exon shuffling. The rice genome contains evidence of numerous gene duplication events facilitated by TE-mediated recombination, with some duplicated genes acquiring new regulatory elements derived from TEs, thereby promoting functional diversification (Gill et.al., 2021).

**C. TEs and Gene Evolution**

**1. Exon shuffling and novel gene creation**
TEs contribute to gene evolution through mechanisms such as exon shuffling, where exonic sequences are mobilized and integrated into new genomic contexts (Nicolau et.al., 2021). Helitrons have been particularly associated with this process, leading to the generation of chimeric genes with novel functions in maize. The capture of gene fragments by TEs can result in the emergence of new genes with altered coding potential or regulatory elements, thereby contributing to phenotypic diversity and adaptive evolution.

**2. Gene regulatory network modification**
TEs often contain regulatory sequences, such as promoters, enhancers, and transcription factor binding sites, which can influence the expression of nearby genes. Retrotransposon insertions within or near gene regulatory regions have been shown to alter gene expression patterns in response to environmental stimuli, providing a substrate for natural selection.

In Arabidopsis, studies have identified that TEs contribute to transcriptional activation of stress-responsive genes by providing novel regulatory elements, highlighting their role in gene network plasticity (Negi et.al., 2016).

**3. Impact on gene expression and gene silencing**
TE insertions within or near coding regions can influence gene expression by providing alternative promoters, disrupting exons, or altering splicing patterns. DNA methylation and histone modifications are commonly used by plant genomes to silence potentially deleterious TE insertions, thereby maintaining genomic stability.

The dynamic regulation of TEs, particularly under environmental stress, can lead to transient activation and subsequent genetic variability that may facilitate adaptation (Song et.al., 2017).

**IV. Transposable Elements and Plant Adaptation**

**A. TEs as Sources of Genetic Diversity**

**1. Stress-induced activation of TEs**
Transposable elements can act as agents of genetic diversity through stress-induced activation. Environmental stresses such as temperature fluctuations, drought, salinity, pathogen attack, and tissue culture conditions have been shown to activate TEs in various plant species. Such activation is believed to result from the relaxation of epigenetic controls, particularly DNA methylation, allowing previously silenced TEs to become transcriptionally active.

In maize (Zea mays), heat stress has been demonstrated to activate the Mutator transposon family, resulting in novel insertions that contribute to phenotypic diversity (Guo et.al., 2021). Stress-induced activation of TEs has also been observed in rice (Oryza sativa) where tissue culture conditions led to the mobilization of Tos17, an LTR retrotransposon, resulting in new insertions within the genome.

**2. Environmental adaptation through TE mobilization**
TE mobilization can create genetic variation that facilitates rapid adaptation to changing environmental conditions. Studies have shown that TEs can influence the expression of stress-responsive genes by inserting near regulatory regions or by donating transcription factor binding sites that enhance gene expression under stress conditions.

In Arabidopsis thaliana, transposon insertions have been linked to gene expression changes in response to biotic and abiotic stresses (Negi et.al., 2016). The insertion of ONSEN, an LTR retrotransposon, is activated by heat stress, leading to its mobilization and the potential creation of novel regulatory networks. Such mechanisms highlight the ability of TEs to contribute to plant resilience and adaptation by generating heritable genetic diversity.

**B. Regulation of Gene Expression via TEs**

**1. TE-derived regulatory elements (promoters, enhancers)**
Transposable elements are not only sources of genetic variation but also contribute to the regulation of gene expression by donating regulatory sequences (Schrader et.al., 2019). These sequences include promoters, enhancers, insulators, and transcription factor binding sites that can alter gene expression patterns and provide novel regulatory inputs. LTR retrotransposons, in particular, contain promoter elements within their long terminal repeats, which can act as alternative promoters for nearby genes. Studies in maize have identified that TE-derived promoters are capable of driving the expression of stress-responsive genes, suggesting a potential role in enhancing plant adaptability under adverse conditions.

**2. Influence on transcriptional and post-transcriptional regulation**
TE insertions can affect transcriptional regulation by providing novel promoters or disrupting existing gene regulatory regions (Fueyo et.al., 2022). Post-transcriptional regulation can also be influenced by TEs through the generation of non-coding RNAs or interference with RNA splicing. In rice, the mPing transposon has been shown to insert near regulatory genes, influencing their expression profiles and contributing to genetic diversity within cultivated and wild populations. TE-mediated gene regulation is increasingly recognized as an important mechanism underlying plant adaptation to environmental changes.

**C. Epigenetic Control of TEs in Adaptation**

**1. DNA methylation and histone modifications**
Epigenetic mechanisms play critical roles in controlling TE activity, particularly through DNA methylation and histone modifications (Dogan et.al., 2021). DNA methylation at cytosine residues is a common silencing mechanism employed by plants to suppress TE transcription and prevent genomic instability. In Arabidopsis, studies have shown that DNA methylation targets LTR retrotransposons and prevents their mobilization. Mutations in DNA methylation pathways often lead to the reactivation of silenced TEs, resulting in increased genetic variation that may be beneficial under certain environmental conditions. Histone modifications, including histone methylation (e.g., H3K9me2) and acetylation, also play essential roles in regulating TE activity (Zhou et.al., 2010). Such modifications are often associated with heterochromatin formation, which effectively silences TEs and protects genome integrity.

**2. Small RNA-mediated silencing**
Small RNAs (sRNAs) are key regulators of TE activity in plants. The RNA-directed DNA methylation (RdDM) pathway involves 24-nucleotide sRNAs that guide DNA methylation at TE loci, ensuring their transcriptional repression. Studies in maize have demonstrated that TE-derived sRNAs are enriched in heterochromatic regions, suggesting their involvement in maintaining genome stability by silencing TEs through RdDM (Erdmann et.al., 2020).

**D. Case Studies of TEs in Plant Adaptation**

**1. Examples from model plants (e.g., Arabidopsis, rice, maize)**
Arabidopsis thaliana serves as a model system for understanding TE regulation and adaptation (Baduel et.al., 2021). The heat-activated ONSEN retrotransposon is an example of stress-induced mobilization contributing to novel genetic variation. In rice, the mobilization of the mPing transposon under stress conditions has been associated with generating new alleles that enhance environmental adaptability. Maize has been extensively studied for TE-induced genome evolution (Lai et.al., 2017). The high abundance of LTR retrotransposons in maize is believed to have contributed significantly to its large genome size and the creation of regulatory diversity, particularly in response to biotic and abiotic stress.

**2. Examples from wild and domesticated plant species**
Wild and domesticated plant species exhibit distinct TE activity patterns that correlate with adaptation to specific ecological niches. In wild rice (*Oryza rufipogon*), for example, TE insertions have been linked to gene regulatory changes that enhance tolerance to submergence and other environmental stresses. Studies on sunflower (Helianthus annuus) have identified that bursts of LTR retrotransposon activity are associated with domestication and adaptation to various climates, indicating a role for TEs in shaping phenotypic diversity (Hassan et.al., 2024).

**V. Evolutionary Implications of TE-Plant Interactions**

**A. TEs as Drivers of Rapid Evolution**

Transposable elements (TEs) are widely recognized as potent drivers of rapid evolution due to their capacity to induce genetic variation, genome restructuring, and novel gene regulation mechanisms. Their ability to create mutations, modify gene expression, and influence gene networks under stress conditions makes them significant contributors to plant adaptation and speciation.

Studies have shown that bursts of TE activity are often associated with major evolutionary transitions in plants (Bennetzen et.al., 2014). In maize (Zea mays), rapid genome expansion has been attributed to extensive retrotransposon amplification, particularly the copia and gypsy families, which constitute over 75% of the genome. In rice (Oryza sativa), the mPing transposon has been demonstrated to generate considerable genetic diversity by inserting near or within genes, contributing to phenotypic variation and adaptation.

Comparative genomic analyses have revealed that TE-driven evolution is not limited to cultivated species. Wild relatives of crops often exhibit higher TE activity, which may contribute to their resilience in natural environments. For example, wild sunflower (Helianthus annuus) populations have experienced recurrent bursts of LTR retrotransposon activity, promoting structural variation associated with adaptation to diverse climates.

**B. Balancing TE Activity and Host Genome Integrity**

The relationship between TEs and their host genomes involves a delicate balance (Rebollo et.al., 2012). While TEs are essential sources of genetic novelty, their uncontrolled activity can result in genomic instability and deleterious mutations. Plants have evolved various mechanisms to control TE activity, ensuring that beneficial effects are maximized while harmful consequences are minimized.

DNA methylation is a primary mechanism employed by plants to repress TE activity (Bartels et.al., 2018). In Arabidopsis thaliana, TE silencing is mediated by RNA-directed DNA methylation (RdDM), which involves the generation of small interfering RNAs (siRNAs) that guide methylation of TE loci. This process effectively silences TEs, preventing their transcription and mobilization.

Histone modifications, including H3K9me2 and H3K27me3, are also crucial for maintaining TE silencing. These modifications establish a heterochromatic environment that restricts TE transcription. Disruption of these mechanisms can result in TE reactivation, especially under stress conditions where epigenetic defences may be relaxed.

Another aspect of balancing TE activity involves targeted deletion or truncation of TEs through non-homologous end joining (NHEJ) and illegitimate recombination (Sinzelle et.al., 2009). In rice, studies have shown that illegitimate recombination is responsible for the removal of more than 90% of LTR retrotransposon sequences over evolutionary timescales, contributing to genome size stability.

**C. Co-evolution of TEs and Host Genomes**

The co-evolutionary relationship between TEs and host genomes is characterized by continuous cycles of TE activity, host genome defense, and adaptation. This dynamic interaction plays a fundamental role in shaping genome architecture and functionality.

TEs have been shown to influence the evolution of gene regulatory networks by donating transcription factor binding sites, enhancers, and promoters (Sundaram et.al., 2020). These regulatory elements can be co-opted by host genomes to drive the expression of nearby genes under specific environmental conditions, thereby enhancing adaptability. In maize, for instance, the insertion of TEs near stress-responsive genes has been linked to altered expression patterns that improve environmental resilience.

Epigenetic regulation of TEs also demonstrates a co-evolutionary process. Host genomes have developed sophisticated mechanisms such as RdDM, histone modifications, and chromatin remodeling to limit TE activity. At the same time, TEs have evolved strategies to evade silencing, such as mutations in recognition sequences and the ability to transpose to unmethylated regions of the genome.

The co-evolutionary relationship is evident in the differential regulation of TEs between wild and domesticated plant species (Yu et.al., 2024). Domestication often involves selection for specific traits, which may impact TE activity and silencing mechanisms. Studies have shown that domesticated rice exhibits lower levels of TE activity compared to its wild relatives, likely due to selective breeding practices that favor genetic stability.

**D. TEs in Polyploidy and Hybridization Events**

Polyploidy and hybridization are important evolutionary processes that can trigger bursts of TE activity (Parisod et.al., 2012). The merging of divergent genomes often results in epigenetic reprogramming, which can release TEs from repression, leading to genomic restructuring and novel gene expression patterns.

In wheat (Triticum aestivum), which is an allohexaploid species, the activity of retrotransposons has been shown to increase following polyploidization events. This phenomenon contributes to genome expansion and functional diversification by providing raw material for gene duplication and modification.

Hybridization between closely related species can also result in TE activation. In synthetic hybrids of sunflower (Helianthus annuus × Helianthus petiolaris), transposon mobilization has been linked to genomic instability and the emergence of novel phenotypic traits that may enhance adaptability.

Studies on Nicotiana tabacum, a natural allotetraploid, have revealed that hybridization-induced TE activation can lead to extensive genomic reorganization (Bashir et.al., 2018). TE insertions have been associated with gene expression changes that may facilitate ecological adaptation.

**VI. Applications and Future Directions**

**A. Biotechnological Applications of TEs**

**1. Genome editing tools (e.g., transposon-based vectors)**
Transposable elements have emerged as valuable tools in genome editing and functional genomics due to their ability to insert DNA sequences into specific or random genomic locations (Kidwell et.al., 2001). Transposon-based vectors such as the **Sleeping Beauty (SB)** and **PiggyBac (PB)** systems have been widely used for gene tagging, gene delivery, and mutagenesis in plants and other organisms.

The SB transposon, a reconstructed Tc1/mariner-type DNA transposon, has been successfully applied in various plant systems for genetic modification. It exhibits efficient cut-and-paste transposition and has been utilized for gene delivery in rice (Oryza sativa) and maize (Zea mays), contributing to the creation of insertional mutant libraries for functional genomics studies.

The PB transposon, originally isolated from the cabbage looper moth (Trichoplusiani), is unique in its ability to transpose through a cut-and-paste mechanism without leaving behind residual sequences, making it particularly useful for precise genome editing (Wachtl et.al.,2022). PB-based vectors have been applied to produce stable gene integration in rice and Arabidopsis thaliana, enhancing our understanding of gene function and regulation.

Transposon-based systems are increasingly being integrated with advanced genome-editing technologies such as CRISPR-Cas9, providing novel strategies for targeted gene modification and functional studies.

**2. TE engineering for functional genomics studies**
Engineering TEs for controlled mobilization has become a powerful approach for functional genomics research. Artificially activating TEs allows researchers to induce insertional mutations throughout the genome, facilitating the discovery of genes associated with important traits.

The mPing transposon, an active miniature inverted-repeat transposable element (MITE) derived from rice, has been utilized as a mutagenesis tool due to its high transposition activity and preference for genic regions. This property makes mPing particularly useful for generating gain-of-function mutants and identifying stress-responsive genes.

The ability to harness TEs for gene discovery and regulatory analysis continues to expand, especially with advancements in transposon tagging, activation tagging, and enhancer trapping systems (Jang et.al., 2024).

**B. Harnessing TEs for Crop Improvement**

**1. TE-induced genetic diversity for breeding**
Transposable elements represent a vast reservoir of genetic diversity that can be exploited for crop improvement. The genetic variability generated by TE insertions provides a valuable source of novel alleles that may enhance agronomic traits, including yield, stress tolerance, and disease resistance.

Studies have shown that TE activity is associated with desirable traits in various crops (Najda et.al., 2016). In maize, TE insertions within regulatory regions have been linked to improved drought tolerance and other stress-related traits. The mPing transposon in rice has been shown to generate heritable insertions that contribute to phenotypic diversity, offering the potential for developing improved rice varieties.

TE-induced mutations have also been exploited for developing new cultivars. For example, the activation of Tos17 in rice through tissue culture has generated numerous insertional mutants that have been used for gene function studies and trait improvement.

**2. Potential for stress tolerance and adaptability**
Harnessing TE activity can be a powerful strategy for developing stress-resilient crops (Zenda et.al., 2021). The insertion of TEs near stress-responsive genes or within regulatory regions can alter gene expression profiles, enhancing a plant's ability to cope with abiotic and biotic stresses.

In Arabidopsis, the heat-activated retrotransposon ONSEN has been demonstrated to mobilize under heat stress conditions, potentially creating new genetic variation that could be beneficial for plant adaptation. This phenomenon highlights the potential of using controlled TE activation to enhance stress tolerance in crops.

Biotechnological approaches aimed at stimulating beneficial TE activity or suppressing deleterious insertions through targeted genome editing and epigenetic manipulation hold promise for improving crop resilience and productivity (Chandana et.al., 2022).

**C. Future Research Prospects**

**1. Integration of multi-omics approaches**
Future research on TEs will likely benefit from the integration of multi-omics approaches, including genomics, transcriptomics, epigenomics, and proteomics. Such approaches will provide a comprehensive understanding of TE activity, regulation, and impact on gene networks.

The development of single-cell sequencing technologies offers new opportunities to study TE dynamics at unprecedented resolution. This technique can reveal how TE activity varies among different cell types and tissues, contributing to developmental processes and stress responses.

Comparative genomics approaches are also expected to uncover TE-mediated evolutionary changes across diverse plant species, providing insights into how TEs contribute to genome diversification and adaptation.

**2. Predicting TE activity and its impact on plant genomes**
Predicting TE activity and its consequences remains a significant challenge in plant genomics. Machine learning and artificial intelligence (AI) tools are increasingly being applied to predict TE insertion sites, assess their impact on gene expression, and identify potential regulatory elements derived from TEs (Giassa et.al., 2021).

Developing computational models that can accurately predict TE activity under different environmental conditions will be essential for understanding how TEs contribute to plant adaptation and resilience. Such models may also facilitate the targeted manipulation of TEs for crop improvement.

Future research will likely focus on refining genome-editing technologies to precisely control TE activity, allowing researchers to harness their potential for developing crops with enhanced stress tolerance and agronomic performance.

**Conclusion**

Transposable elements (TEs) are powerful agents of genome evolution, adaptation, and innovation in plants. Their capacity to induce genetic diversity, influence gene expression, and drive structural variations has significantly contributed to plant genome architecture and adaptability. TE activity, particularly under stress conditions, provides a dynamic mechanism for generating beneficial mutations and novel regulatory networks essential for environmental resilience. While plants have evolved sophisticated epigenetic mechanisms to control TE activity, selective activation of TEs can be harnessed for crop improvement through genome editing, functional genomics, and breeding programs. Future research integrating multi-omics approaches and advanced computational models will enhance our understanding of TE dynamics and their evolutionary implications. Leveraging TEs for biotechnological applications presents promising opportunities to enhance stress tolerance, productivity, and adaptability in crops, ultimately contributing to food security and sustainable agriculture.

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**Reference**

1. Kidwell, M. G., & Lisch, D. R. (2001). Perspective: transposable elements, parasitic DNA, and genome evolution. *Evolution*, *55*(1), 1-24.
2. Schmitz, M., & Querques, I. (2024). DNA on the move: mechanisms, functions and applications of transposable elements. *FEBS Open Bio*, *14*(1), 13-22.
3. Negi, P., Rai, A. N., & Suprasanna, P. (2016). Moving through the stressed genome: emerging regulatory roles for transposons in plant stress response. *Frontiers in plant science*, *7*, 1448.
4. Sen, M. K., Hamouzová, K., Roy, A., & Soukup, J. (2024). Transposable element-driven evolution of herbicide resistance in plants. *Journal of Experimental Botany*, erae517.
5. Lee, S. I., & Kim, N. S. (2014). Transposable elements and genome size variations in plants. *Genomics & informatics*, *12*(3), 87.
6. Mangoni, D., Mazzetti, A., Ansaloni, F., Simi, A., Tartaglia, G. G., Pandolfini, L., ... & Sanges, R. (2025). From the genome's perspective: Bearing somatic retrotransposition to leverage the regulatory potential of L1 RNAs. *BioEssays*, *47*(2), 2400125.
7. Hallet, B., & Sherratt, D. J. (1997). Transposition and site-specific recombination: adapting DNA cut-and-paste mechanisms to a variety of genetic rearrangements. *FEMS Microbiology Reviews*, *21*(2), 157-178.
8. Thomas, J., & Pritham, E. J. (2015). Helitrons, the eukaryotic rolling‐circle transposable elements. *Mobile DNA iii*, 891-924.
9. Silva, J. C., Loreto, E. L., & Clark, J. B. (2004). Factors that affect the horizontal transfer of transposable elements. *Current issues in molecular biology*, *6*(1), 57-72.
10. Oliver, K. R., & Greene, W. K. (2009). Transposable elements: powerful facilitators of evolution. *Bioessays*, *31*(7), 703-714.
11. Zuccolo, A., Sebastian, A., Talag, J., Yu, Y., Kim, H., Collura, K., ... & Wing, R. A. (2007). Transposable element distribution, abundance and role in genome size variation in the genus Oryza. *BMC Evolutionary Biology*, *7*, 1-15.
12. Platt, R. N., Vandewege, M. W., & Ray, D. A. (2018). Mammalian transposable elements and their impacts on genome evolution. *Chromosome Research*, *26*(1), 25-43.
13. Oliver, K. R., & Greene, W. K. (2012). Transposable elements and viruses as factors in adaptation and evolution: an expansion and strengthening of the TE‐Thrust hypothesis. *Ecology and evolution*, *2*(11), 2912-2933.
14. Dooner, H. K., & Weil, C. F. (2013). Transposons and gene creation. *Plant transposons and genome dynamics in evolution*, 143-164.
15. Gill, R. A., Scossa, F., King, G. J., Golicz, A. A., Tong, C., Snowdon, R. J., ... & Liu, S. (2021). On the role of transposable elements in the regulation of gene expression and subgenomic interactions in crop genomes. *Critical Reviews in Plant Sciences*, *40*(2), 157-189.
16. Nicolau, M., Picault, N., & Moissiard, G. (2021). The evolutionary volte-face of transposable elements: from harmful jumping genes to major drivers of genetic innovation. *Cells*, *10*(11), 2952.
17. Negi, P., Rai, A. N., & Suprasanna, P. (2016). Moving through the stressed genome: emerging regulatory roles for transposons in plant stress response. *Frontiers in plant science*, *7*, 1448.
18. Song, X., & Cao, X. (2017). Transposon-mediated epigenetic regulation contributes to phenotypic diversity and environmental adaptation in rice. *Current Opinion in Plant Biology*, *36*, 111-118.
19. Guo, W., Wang, D., & Lisch, D. (2021). RNA-directed DNA methylation prevents rapid and heritable reversal of transposon silencing under heat stress in Zea mays. *PLoS Genetics*, *17*(6), e1009326.
20. Negi, P., Rai, A. N., & Suprasanna, P. (2016). Moving through the stressed genome: emerging regulatory roles for transposons in plant stress response. *Frontiers in plant science*, *7*, 1448.
21. Schrader, L., & Schmitz, J. (2019). The impact of transposable elements in adaptive evolution. *Molecular Ecology*, *28*(6), 1537-1549.
22. Fueyo, R., Judd, J., Feschotte, C., & Wysocka, J. (2022). Roles of transposable elements in the regulation of mammalian transcription. *Nature reviews Molecular cell biology*, *23*(7), 481-497.
23. Dogan, F., & Forsyth, N. R. (2021). Telomerase regulation: a role for epigenetics. *Cancers*, *13*(6), 1213.
24. Zhou, J., Wang, X., He, K., Charron, J. B. F., Elling, A. A., & Deng, X. W. (2010). Genome-wide profiling of histone H3 lysine 9 acetylation and dimethylation in Arabidopsis reveals correlation between multiple histone marks and gene expression. *Plant molecular biology*, *72*, 585-595.
25. Erdmann, R. M., & Picard, C. L. (2020). RNA-directed DNA methylation. *PLoS genetics*, *16*(10), e1009034.
26. Baduel, P., Leduque, B., Ignace, A., Gy, I., Gil Jr, J., Loudet, O., ... & Quadrana, L. (2021). Genetic and environmental modulation of transposition shapes the evolutionary potential of Arabidopsis thaliana. *Genome biology*, *22*(1), 138.
27. Lai, X., Schnable, J. C., Liao, Z., Xu, J., Zhang, G., Li, C., ... & Lu, Y. (2017). Genome-wide characterization of non-reference transposable element insertion polymorphisms reveals genetic diversity in tropical and temperate maize. *BMC genomics*, *18*, 1-13.
28. Hassan, A. H., Mokhtar, M. M., & El Allali, A. (2024). Transposable elements: multifunctional players in the plant genome. *Frontiers in Plant Science*, *14*, 1330127.
29. Bennetzen, J. L., & Wang, H. (2014). The contributions of transposable elements to the structure, function, and evolution of plant genomes. *Annual review of plant biology*, *65*(1), 505-530.
30. Rebollo, R., Romanish, M. T., & Mager, D. L. (2012). Transposable elements: an abundant and natural source of regulatory sequences for host genes. *Annual review of genetics*, *46*(1), 21-42.
31. Bartels, A., Han, Q., Nair, P., Stacey, L., Gaynier, H., Mosley, M., ... & Xiao, W. (2018). Dynamic DNA methylation in plant growth and development. *International journal of molecular sciences*, *19*(7), 2144.
32. Sinzelle, L., Izsvak, Z., & Ivics, Z. (2009). Molecular domestication of transposable elements: from detrimental parasites to useful host genes. *Cellular and molecular life sciences*, *66*, 1073-1093.
33. Sundaram, V., & Wysocka, J. (2020). Transposable elements as a potent source of diverse cis-regulatory sequences in mammalian genomes. *Philosophical Transactions of the Royal Society B*, *375*(1795), 20190347.
34. Yu, Z., Li, J., Wang, H., Ping, B., Li, X., Liu, Z., ... & Zhao, T. (2024). Transposable elements in Rosaceae: insights into genome evolution, expression dynamics, and syntenic gene regulation. *Horticulture Research*, *11*(6), uhae118.
35. Parisod, C., & Senerchia, N. (2012). Responses of transposable elements to polyploidy. *Plant transposable elements: impact on genome structure and function*, 147-168.
36. Bashir, T., Chandra Mishra, R., Hasan, M. M., Mohanta, T. K., & Bae, H. (2018). Effect of hybridization on somatic mutations and genomic rearrangements in plants. *International journal of molecular sciences*, *19*(12), 3758.
37. Kidwell, M. G., & Lisch, D. R. (2001). Perspective: transposable elements, parasitic DNA, and genome evolution. *Evolution*, *55*(1), 1-24.
38. Wachtl, G., Schád, É., Huszár, K., Palazzo, A., Ivics, Z., Tantos, Á., & Orbán, T. I. (2022). Functional characterization of the N-Terminal disordered region of the piggyBac transposase. *International Journal of Molecular Sciences*, *23*(18), 10317.
39. Jang, H. J., Shah, N. M., Maeng, J. H., Liang, Y., Basri, N. L., Ge, J., ... & Wang, T. (2024). Epigenetic therapy potentiates transposable element transcription to create tumor-enriched antigens in glioblastoma cells. *Nature Genetics*, *56*(9), 1903-1913.
40. Najda, A., Błaszczyk, L., Winiarczyk, K., Dyduch, J., & Tchórzewska, D. (2016). Comparative studies of nutritional and health-enhancing properties in the “garlic-like” plant Allium ampeloprasum var. ampeloprasum (GHG-L) and A. sativum. *Scientia Horticulturae*, *201*, 247-255.
41. Zenda, T., Liu, S., Dong, A., Li, J., Wang, Y., Liu, X., ... & Duan, H. (2021). Omics-facilitated crop improvement for climate resilience and superior nutritive value. *Frontiers in Plant Science*, *12*, 774994.
42. Chandana, B. S., Mahto, R. K., Singh, R. K., Ford, R., Vaghefi, N., Gupta, S. K., ... & Kumar, R. (2022). Epigenomics as potential tools for enhancing magnitude of breeding approaches for developing climate resilient chickpea. *Frontiers in Genetics*, *13*, 900253.
43. Giassa, I. C., & Alexiou, P. (2021). Bioinformatics and machine learning approaches to understand the regulation of mobile genetic elements. *Biology*, *10*(9), 896.
44. 44. Benoit, M., Drost, H. G., Catoni, M., Gouil, Q., Lopez-Gomollon, S., Baulcombe, D., et al. (2019). Environmental and epigenetic regulation of rider retrotransposons in tomato. PloS Genet. 15, 1–28. doi: 10.1371/journal.pgen.1008370Kaur, S., Seem, K., Vinod, K. K., Mishra, D. C., Kumar, S., & Mohapatra, T. (2024). Comparative RNA-seq analysis reveals transposable element-mediated transcriptional reprogramming under phosphorus-starvation stress in rice (Oryza sativa L.). Gene Reports, 37, 102077.
45. Saha , Sajal, Deepa Bhadana, Pankaj Kumar Shah, H. P. Chaturvedi, P. N. Verma, Rajib Das, Rinkey Arya, Pravesh Kumar, Sagar Agarwal, and D. Purushotama Rao. 2023. “Genoplasmics: Advancing Plant Germplasm Research through Genomics”. *International Journal of Plant & Soil Science* 35 (21):106-16. <https://doi.org/10.9734/ijpss/2023/v35i213951>.
46. Ndlovu, Noel. 2020. “Application of Genomics and Phenomics in Plant Breeding for Climate Resilience”. *Asian Plant Research Journal* 6 (4):53-66. https://doi.org/10.9734/aprj/2020/v6i430137.