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Review paper

Transposable elements: mechanistic insights into a dynamic regulatory landscape of plant stress response with agricultural implications

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Abstract: Transposable genetic elements (TEs) are dynamic DNA sequences that significantly impact plant gene expression, enabling adaptation to environmental stresses. This review explores the role of TEs in plant adaptation, focusing on the mechanisms of TE activation and suppression, including chromatin remodeling, DNA modifications, and small interfering RNAs (siRNAs). Stress conditions trigger TE activation through interactions between stress-induced transcription factors and TE promoters, as seen with retrotransposon families like COPIA93 and ONSEN in modulation of stress-responsive genes. Understanding these mechanisms provides valuable insights for agriculture, particularly in developing crops that are resilient to climate change. Leveraging TE-mediated gene regulation presents innovative strategies for enhancing plant adaptation, highlighting the potential of TEs in genetic manipulation for plant improvement.

Keywords: Transposable elements, epigenetic regulation, environmental adaptation, noncoding RNAs, plant stress.

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Introduction

Epigenetic research has demonstrated that heritable modifications in gene function, which do not include any changes to the DNA sequence, play a crucial role in plants' ability to adapt to environmental stress (Kakoulidou *et al.,* 2021; Hoseini and Arzani, 2023; Hoseini *et al.,* 2024). Epigenetics refers to these heritable changes in gene activity that do not involve changes to the underlying DNA sequence. The alterations mentioned above, which are facilitated by several processes including DNA methylation, histone modification, and RNA interference, highlight the inherent adaptability of plant genomes in reaction to external stimuli (Akhter *et al.,* 2021). Transposable elements (TEs) are dynamic DNA sequences found in both eukaryotic and prokaryotic genomes. TEs have the ability to move within the genome, introducing genetic variations that significantly impact gene expression and contribute to plant adaptability (Fambrini *et al.,* 2020; Ramakrishnan *et al.,* 2022). These variations help plants to cope with both biotic and abiotic stressors. Abiotic stress refers to the negative impact of non-living factors, such as drought, salinity, and extreme temperatures, on plants (Hoque *et al.,* 2020). TEs were historically considered genomic parasites; however, recent research has highlighted their crucial role in genome evolution and stress adaptation (Pandita and Pandita, 2023). The responsibilities of TEs go beyond their function as genetic disruptors. They actively engage in epigenetic regulation, which enables plants to respond to environmental challenges by modifying chromatin, integrating regulatory sequences, and producing noncoding RNA (Mozgova *et al.,* 2019; Klein and Anderson, 2022). Recent advancements in cutting-edge technologies, such as CRISPR-based tools, have significantly advanced TE research by allowing precise manipulation and investigation of TEs, further uncovering their roles in plant resilience (Zhang *et al.,* 2022).

This review emphasizes the evolutionary importance of TEs and specifically examines their influence on gene expression under abiotic stress conditions. This study also explores recent research that highlights the significance of TEs, which were previously regarded as genomic parasites, in relation to their crucial role in enhancing plant adaptability and survival across many settings. The narrative commences by acknowledging Barbara McClintock's groundbreaking research (McClintock, 1950), which revealed the dynamic characteristics of TEs, establishing the foundation for our present comprehension of their essential function in the evolution and functioning of plant genomes, specifically under stress conditions (Pulido and Casacuberta, 2023).

TEs have been extensively studied and found to play a significant role in the development and operation of the host genome, specifically in how plants respond to environmental challenges (Ramakrishnan *et al.,* 2022). In general, TEs have a role in regulating genes and modifying gene responses to their surroundings, hence influencing the dynamics of the genome (Schrader and Schmitz, 2019; Diehl *et al.,* 2020). Studies have demonstrated that TEs occupy several functions within plant genomes. The mechanisms above encompass the facilitation of gene duplication or deletion, the modulation of gene expression or activity, and the amalgamation of genes from disparate sites into innovative combinations (Gill *et al.,* 2021). TEs interfere with the functioning of genes by infiltrating genes or gene regulatory elements. They can induce chromosomal rearrangements by undergoing aberrant recombination between numerous TE copies (Almojil *et al.,* 2021).

To quickly and consistently adapt to environmental changes, plants need a high degree of growth flexibility, which enables them to flourish diverse and unfamiliar conditions (Majid *et al.,* 2017). The presence of genetic variation across plant populations has been found to augment their ability to withstand both biotic and abiotic challenges (Ghasemi-Soloklui *et al.,* 2023). According to the selfish DNA theory, TEs have been conserved on different chromosomes throughout the evolutionary history of plants, exhibiting significant variations in terms of quantity, variety, and positioning (Kent, 2023). The content of TEs in plant genomes varies greatly, ranging from a minimum of 3% in aquatic plants such as *Utricularia gibba* to more than 85% in complex polyploids like wheat (Pegler *et al.,* 2023). Our objective is to gain insight into the delicate equilibrium between genomic stability and flexibility, which is crucial for plant resilience in response to shifting environmental conditions. This study presents a synthesis of recent research findings regarding the roles of TEs in facilitating changes in gene expression during periods of stress, and discusses their implications for future agricultural applications. As a result, it contributes to the wider academic conversation surrounding plant adaptation techniques.

Transposable elements: An epigenetic perspective

TEs play a critical role in the epigenetic regulation of plant genomes, offering a unique lens to understand how plants adapt to stress (Figure 1). Classified broadly into 'copy and paste' (Class I, or Retrotransposons) and 'cut and paste' (Class II, DNA transposons), these elements contribute to genomic diversity and flexibility (Wells and Feschotte, 2020). Class I TEs replicate through an RNA intermediary, a process involving transcription to RNA followed by reverse transcription back into DNA, facilitated by reverse transcriptase enzymes. These are prevalent in large plant genomes and include subtypes with long terminal repeats (LTRs) and those without, impacting genome structure and function differently (Kojima, 2019).

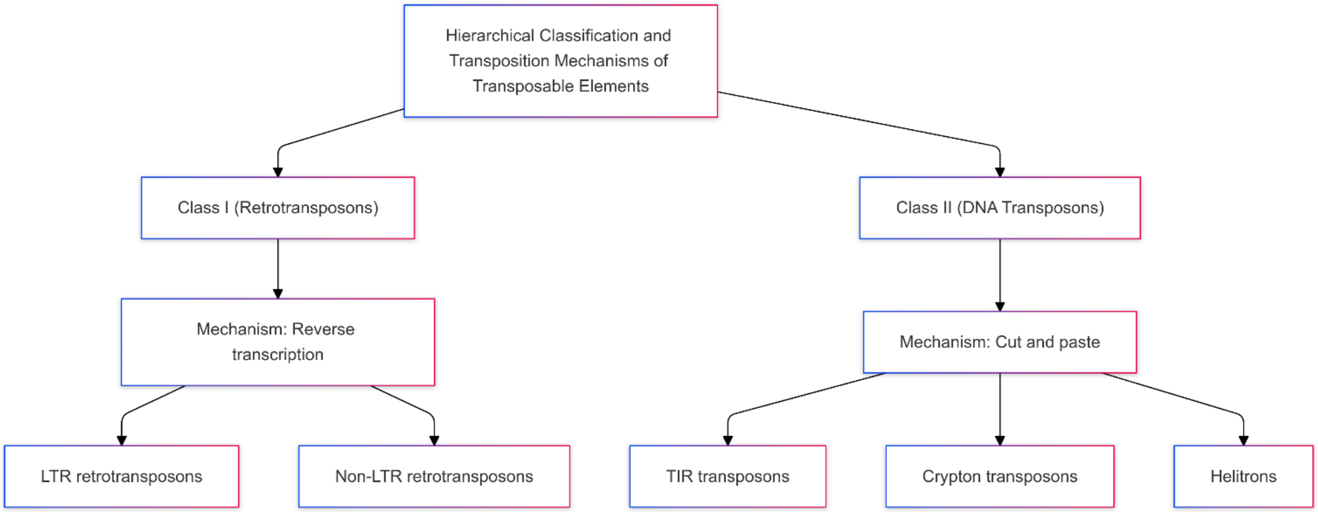

Figure 1. Classification of transposable elements in eukaryotes. This figure provides an overview of the different classes and subclasses of transposable elements, helping to establish a foundation for understanding their diverse roles and mechanisms within eukaryotic genomes.

On the other hand, Class II TEs, found across eukaryotes, maneuver through a direct 'cut and paste' mechanism, enabling them to move autonomously within the genome. This movement, governed by the transposase enzyme, adds to the genetic diversity essential for plants' stress adaptation mechanisms (Schrader and Schmitz, 2019; Bhat *et al.*, 2022).

Both autonomous and non-autonomous TEs, with the former capable of independent relocation and the latter requiring assistance from autonomous elements, enrich the plant's response to environmental changes. The variety in TE size and encoded genes underscores their complexity and influence on plant genome architecture. For example, TEs make up significant portions of the genome in many plants, such as around 85% in maize, with varying impacts on gene expression and regulation (Oliver *et al.*, 2013; Jouffroy *et al.*, 2016; Quesneville, 2020; Ramakrishnan *et al.*, 2021). In sum, TEs are not just genomic relics but active participants in shaping gene expression and plant adaptation to stress through epigenetic mechanisms.

Mechanisms of transposable element activation and silencing

TEs undergo strict regulation to balance their contributions to genetic diversity against the risk of genomic instability (Kremer *et al.*, 2020). Activation of TEs is often triggered by environmental stressors, developmental cues, or certain phases of the life cycle, enhancing genetic variability crucial for plant adaptation (Figure 2) (Mustafin and Khusnutdinova, 2019). For example, under drought stress, the frequency of activated TEs in maize was found to increase significantly, highlighting the role of environmental factors in triggering TE activity (Makarevitch *et al.*, 2015). However, unregulated TE activity can threaten genomic integrity, necessitating robust mechanisms for their repression (Almojil *et al.*, 2021).

Activation mechanisms

External stresses—such as temperature fluctuations, drought, and pathogen invasion—can prompt TE activation by altering the cellular environment and epigenetic status, initiating transcription. For instance, the ONSEN retrotransposon in *Arabidopsis* becomes active under heat stress, potentially facilitating adaptation (Nozawa *et al.*, 2022). Quantitative data also indicate that the frequency of ONSEN copies increases significantly—up to tenfold—under repeated heat stress conditions, demonstrating transgenerational effects (Ito *et al.*, 2016). Developmental signals, particularly during gametogenesis and embryogenesis, can also increase TE activity, enriching genetic diversity in progeny (Maupetit-Mehouas and Vaury, 2020).

Silencing mechanisms

DNA methylation, histone modifications, and RNA interference (RNAi) are epigenetic controls that rely heavily on TE suppression (Choi and Lee, 2020). Different researchers found that DNA methyltransferases are essential for DNA methylation at TE promoters, which inhibits TE transcription (Deniz *et al.*, 2019; Domb *et al.*, 2020)..

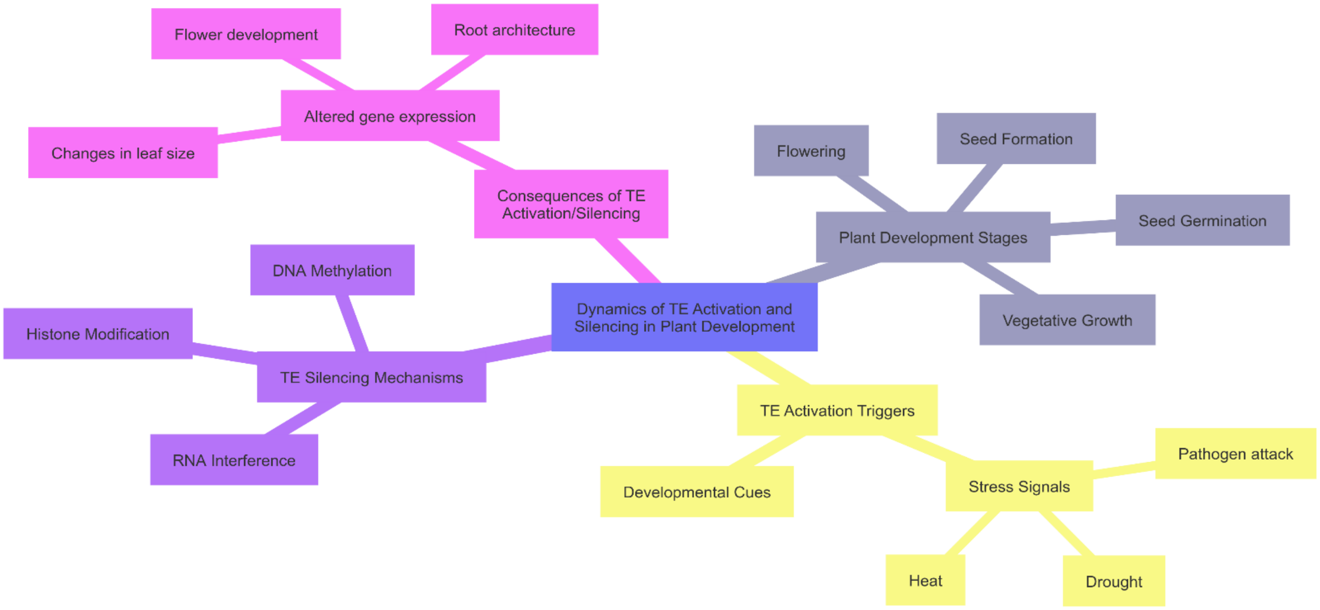

Figure 2. Dynamics of TE activation and silencing in plant development. This figure illustrates the processes of TE activation and silencing, showing how these elements are regulated during different stages of plant development and in response to environmental cues. It supports the discussion on the balance between TE activity and repression, contributing to plant adaptability.

Quantitative analysis has shown that in stressed versus unstressed conditions, levels of DNA methylation at TE sites can decrease significantly, corresponding to increased TE activity during stress (Secco *et al.*, 2015). Heterochromatin formation and TE silencing are both impacted by histone modifications, such as H3 lysine 9 dimethylation (H3K9me2) (Underwood and Choi, 2019). The RNA-directed DNA methylation (RdDM) pathway is essential for maintaining TE suppression by specifically methylating TE sequences; RNA interference (RNAi) mechanisms also produce small noncoding RNAs that target TEs for silencing (Erdmann and Picard, 2020).

Dynamic balance

The equilibrium between TE activation and suppression underscores the plant genome's adaptability and stability. While activation under stress can introduce beneficial traits for stress tolerance, robust silencing mechanisms ensure genomic stability is restored post-stress (Liu *et al.*, 2022). For example, studies have shown that after stress conditions subside, TE silencing is reestablished within a few cell cycles, reducing the frequency of TE transcription events compared to peak activation levels (Naito *et al.*, 2009). This dynamic interplay between activation and silencing mechanisms allows plants to adapt to changing environments without compromising genomic integrity

Transposable elements as epigenetic regulators

TEs extend beyond their mobility within the genome, playing pivotal roles in epigenetic regulation (Figures 3 and 4). These elements significantly influence genome responsiveness to environmental stimuli, underpinning adaptability and evolutionary processes (Nishihara, 2019; Colonna Romano and Fanti, 2022). TEs modulate epigenetic landscapes through several mechanisms (Figure 4): they alter DNA methylation patterns, reshape histone configurations, and generate noncoding RNAs, each contributing to the complexity of gene regulation (Ali *et al.*, 2021). Notably, similar regulatory roles of TEs have been observed in other eukaryotes, including animals and fungi, where TEs contribute to chromatin modifications and influence stress responses (Slotkin and Martienssen, 2007; Rebollo *et al.*, 2010).

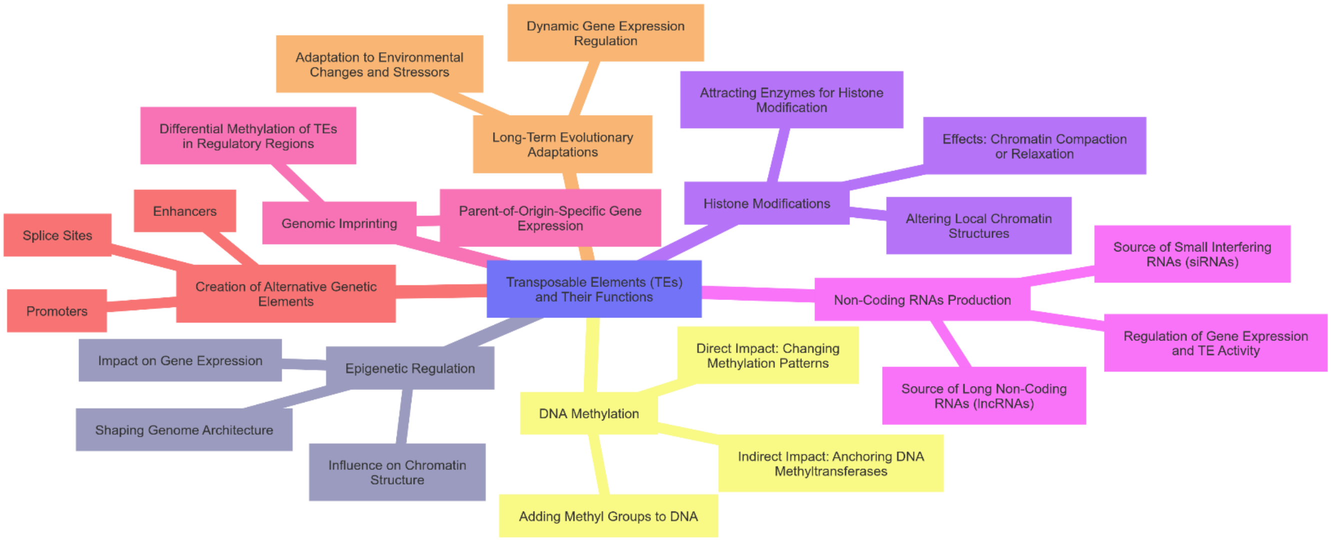

Figure 3. The mind map diagram illustrating the roles and functions of Transposable Elements (TEs). This diagram offers a comprehensive overview of the multiple roles that TEs play in genome evolution, gene regulation, and stress response, reinforcing the detailed discussion provided in the text.

DNA methylation

TEs directly influence the DNA methylation landscape, with their integration altering methylation patterns near or within genes, potentially leading to changes in gene activity. They also serve as platforms for DNA methyltransferases, indirectly modulating genome-wide methylation and affecting gene expression, particularly in stress responses and development (Deniz *et al.*, 2019; Kumar and Rani, 2023).

Histone modifications

A change in local chromatin architecture can occur as a result of TE integration into the genome, which attracts enzymes that modify histones. Their ability to methylate, acetylate, and ubiquitinate histones impacts the transcription machinery's ability to access DNA. For example, under drought stress, TEs have been shown to promote H3K9me2 (histone H3 lysine 9 dimethylation), leading to the formation of heterochromatin and suppression of nearby genes (Bej and Basak, 2017). Conversely, heat stress can induce H3K27ac (histone H3 lysine 27 acetylation), resulting in the activation of TEs and adjacent genes, aiding in plant adaptation (Korotko *et al.*, 2021). According to (Drongitis *et al.*, 2019; Bousios *et al.*, 2020), the presence of TEs can induce either a chromatin state that silences genes or an activating one.

Noncoding RNAs

Long noncoding RNAs (lncRNAs) and small interfering RNAs (siRNAs) also originate from TEs. These molecules are essential for gene regulation; lncRNAs may influence gene expression close to TEs, and siRNAs silence particular genes or TEs. This ability to regulate adds a new layer to epigenetic regulation, which affects mechanisms of stress response and development (Ariel and Manavella, 2021; Gebrie, 2023).

Genomic imprinting and regulatory element formation

Beyond these mechanisms, TEs contribute to genomic imprinting by differentially methylating regulatory regions of imprinted genes. They also foster genomic diversity by creating alternative promoters, enhancers, and splice sites, enhancing the functional repertoire of the genome (Batista and Köhler, 2020; Gill *et al.*, 2021).

TEs' role as epigenetic regulators is central not only to immediate environmental response but also to long-term evolutionary adaptation. By influencing epigenetic modifications, TEs enable dynamic regulation of gene expression, facilitating organismal adaptation to changing environments and stressors. This underscores the significance of TEs not only in plants but also across other eukaryotic organisms, where they offer mechanisms for rapid genomic adaptation to new challenges (Slotkin and Martienssen, 2007; Klein and Anderson, 2022). This underscores TEs' integral role in the evolutionary narrative, offering mechanisms for rapid genomic adaptation to new challenges (Baduel and Quadrana, 2021; Klein and Anderson, 2022).

Evolutionary perspectives of transposable elements

The presence of TEs has played a crucial role in influencing the evolutionary path of plant genomes (Colonna Romano and Fanti, 2022). TEs play a crucial role in genomic innovation, promoting diversity and complexity throughout the plant kingdom, rather than being only genetic curiosities (Pandita and Pandita, 2023). The relevance of their involvement in evolution is underscored by their ability to introduce new genetic material, facilitate gene and genome duplications, and contribute to the formation of novel regulatory networks (Bhat *et al.*, 2022).

TEs are dynamic elements of the genome that can generate new genomic arrangements (Stitzer *et al.*, 2021). The capacity to relocate and integrate into diverse genomic sites facilitates the incorporation of novel genetic material. The ability to move has made it easier for genes with new functions to develop and for gene families to grow, which has improved the ability of plants to adapt (Ramakrishnan *et al.*, 2021). For example, in wheat (*Triticum aestivum*), a hexaploid species, TEs have played a key role in polyploid genome evolution. The rapid amplification of TEs contributed to genome expansion and facilitated adaptive traits such as increased resilience to stress conditions, including cold and drought (Wicker, 2018).

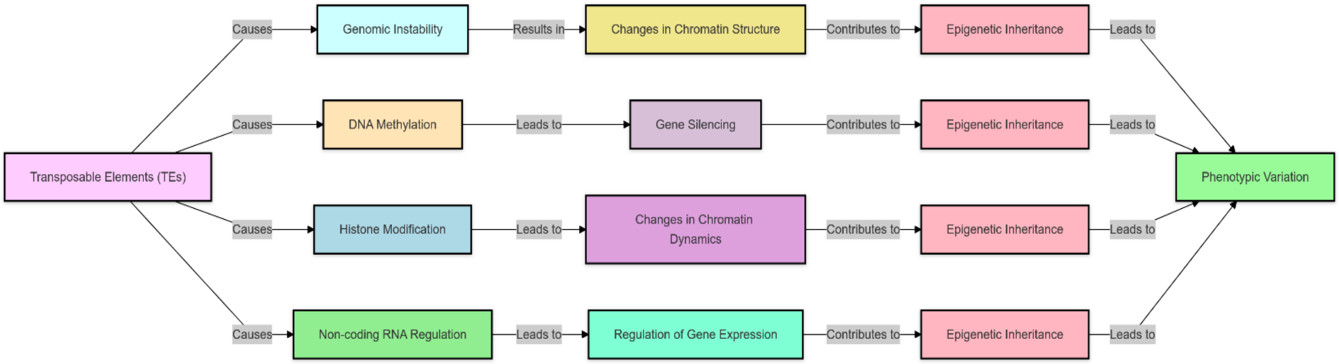

Figure 4. A flowchart diagram illustrating the epigenetic modifications mediated by Transposable Elements (TEs). This figure explains how TEs influence epigenetic modifications, such as DNA methylation and histone changes, emphasizing their role in gene regulation and chromatin structure.

The correlation between the abundance of TEs in the maize genome and its notable genetic variability has been shown, hence playing a role in the development of traits such as stress tolerance and nutrient utilization efficiency (Stitzer *et al.*, 2021).

Gene duplication events, frequently facilitated by transposable elements (TEs), serve as a fundamental origin of novel genetic material inside plant genomes. Transposable elements (TEs) can promote these duplications by interfering with each other or by acting as templates for the replication of neighboring genomic segments (Gill *et al.*, 2021). Polyploidy, also known as genome duplication, is a pivotal evolutionary occurrence in plants, serving as a fundamental catalyst for evolutionary advancements (Wang *et al.*, 2021). In wheat, polyploidy is associated with extensive TE activity, which has been linked to both gene loss (nonfunctionalization) and the evolution of new gene functions (neofunctionalization) that enhance adaptability to diverse environments (Wicker, 2018). TEs have been associated with the structural changes that occur during polyploidy, allowing for both the nonfunctionalization and long-term neofunctionalization and subfunctionalization of duplicate genes (Fambrini *et al.*, 2020).

The introduction of new promoters, enhancers, and silencers by TEs has been crucial in the evolution of gene regulation networks (Palazzo and Marsano, 2021). These factors can modify the way genes are expressed, resulting in the expansion of regulatory pathways and the creation of intricate developmental processes (Kakoulidou *et al.*, 2021). The enduring influence of TE-derived regulatory sequences on gene regulation is demonstrated by their presence in plant promoters (Hannan Parker *et al.*, 2022).

The adaptive flexibility given by TEs contributes to the evolutionary success of plants. Through the production of genetic diversity, TEs facilitate the ability of plants to swiftly adjust to shifting environmental circumstances. In maize (*Zea mays*), specific TEs have been linked to the adaptation of plants to different climatic conditions by modulating gene expression related to drought and nutrient stress (Makarevitch *et al.*, 2015). The ability to adapt is essential for the survival and diversification of plants, enabling them to establish themselves in new ecological areas and develop into unique species (Baduel and Quadrana, 2021). The importance of TEs on plant diversity is underscored by their involvement in generating sympatric speciation, which refers to the emergence of new species from a single ancestral species while residing in the same geographic region.

Molecular tools and techniques

TEs exert epigenetic influences, and recent developments in molecular methodologies have revolutionized our understanding of their role in genomic regulation and adaptation (Baduel *et al.*, 2021). These advancements include the novel CRISPR-Cas system for targeted epigenetic modifications, sophisticated sequencing technologies, and a set of methods for analyzing TE-driven epigenetic changes (Mohan *et al.*, 2022).

Techniques for studying epigenetic effects of transposable elements

In-depth molecular analysis techniques and advanced methodologies are necessary to analyze the epigenetic roles of TEs. One essential method for studying DNA methylation is bisulfite sequencing (Chen *et al.*, 2022). This process involves treating DNA with sodium bisulfite, which turns unmethylated cytosines into uracil while protecting methylated cytosines. The resulting sequencing data can shed light on epigenetic modifications brought about by TEs by providing information on the methylation status throughout the entire genome (Urich *et al.*, 2015). Chromatin immunoprecipitation followed by sequencing (ChIP-seq) is another essential method that is used to examine histone modifications close to translocations (TEs). This technique highlights the impact of TEs on chromatin architecture and gene regulation by isolating and sequencing genomic regions linked to different histone marks using particular antibodies that target modified histones (Lerat *et al.*, 2019).

Clarifying how TEs impact gene expression has also been made possible by RNA sequencing, or RNA-seq (Wang *et al.*, 2017). RNA-seq offers a comprehensive view of the transcriptome by measuring and sequencing RNA transcripts. It also demonstrates how TEs may impact alterations in gene expression through epigenetic mechanisms (Stuart, 2018). Furthermore, the increasing use of ATAC-seq (Assay for Transposase-Accessible Chromatin with high-throughput sequencing) to assess chromatin accessibility sheds more light on the role of TEs in altering the chromatin environment (Bourguet *et al.*, 2021).

CRISPR-Cas system in epigenetic editing

Initially identified as a bacterial defense strategy, the CRISPR-Cas system has been repurposed into a potent genome and epigenome editing tool (Jogam *et al.*, 2022). This technology facilitates precise DNA sequence modifications, including areas around TEs (Merkulov *et al.*, 2023). By leveraging this system, researchers can intentionally modify epigenetic marks at specific TE sites, enabling them to probe their influence on gene regulation and chromatin structure (Liu *et al.*, 2022). The CRISPR-Cas system is adept at directing epigenetic modifiers to particular genomic regions, allowing the investigation of the direct and reversible impacts of epigenetic alterations (Selma and Orzáez, 2021). This precision editing paves the way for unraveling the interplay between TE activities, epigenetic changes, and resultant phenotypic effects (Kirov, 2023).

CRISPR-Cas has also evolved to enable epigenetic modifications without changing the DNA sequence . By inactivating the nuclease function of Cas9 (dCas9) and fusing it with enzymes that alter DNA methylation or histones, researchers can target specific epigenetic changes to TE regions. This innovative use of CRISPR-dCas9 offers unparalleled control over the epigenetic state of TEs, facilitating in-depth analyses of their role in gene expression regulation and genomic variation (Shin *et al.*, 2022).

Advances in epigenomic sequencing technologies

The field of epigenomics has advanced significantly as a result of the development of high-throughput sequencing technologies (Gogolev *et al.*, 2021). The whole genome's epigenetic modifications can now be comprehensively mapped thanks to these technologies (Figure 5). The application of next-generation sequencing (NGS) platforms has led to significant cost savings and improvements in sequencing productivity, which has made extensive studies of epigenetics possible (Kulski, 2016). With methods like whole-genome bisulfite sequencing (WGBS), comprehensive maps of DNA methylation can be obtained throughout the entire genome, including TE regions. By applying this methodology, researchers can link methylation patterns to phenotypic traits and gene expression (Omony *et al.*, 2020).

Additionally, the field of epigenetic research is expanding with the use of third-generation sequencing technologies like single-molecule real-time (SMRT) and nanopore sequencing. These technologies' longer read lengths allow for the simultaneous sequencing of TEs and the areas around them (Usha *et al.*, 2022). This feature is useful for studying TEs, which often show repetitive patterns and are challenging to analyze with short-read sequencing methods. The application of long-read sequencing methods advances our knowledge of the intricate genomic terrain sculpted by transposons and the corresponding epigenetic changes (Shahid and Slotkin, 2020).

In parallel with these sequencing advancements, developments in computational biology have been essential in interpreting the extensive data generated. Bioinformatics tools and algorithms are continually refined to analyze epigenetic data, offering insights into the dynamic interactions between TEs and the epigenome (Pandita and Pandita, 2023). These tools facilitate the integration of diverse data types, such as DNA methylation, histone modification, and RNA expression, creating a holistic view of the epigenetic influences exerted by TEs (Ramakrishnan *et al.*, 2022).

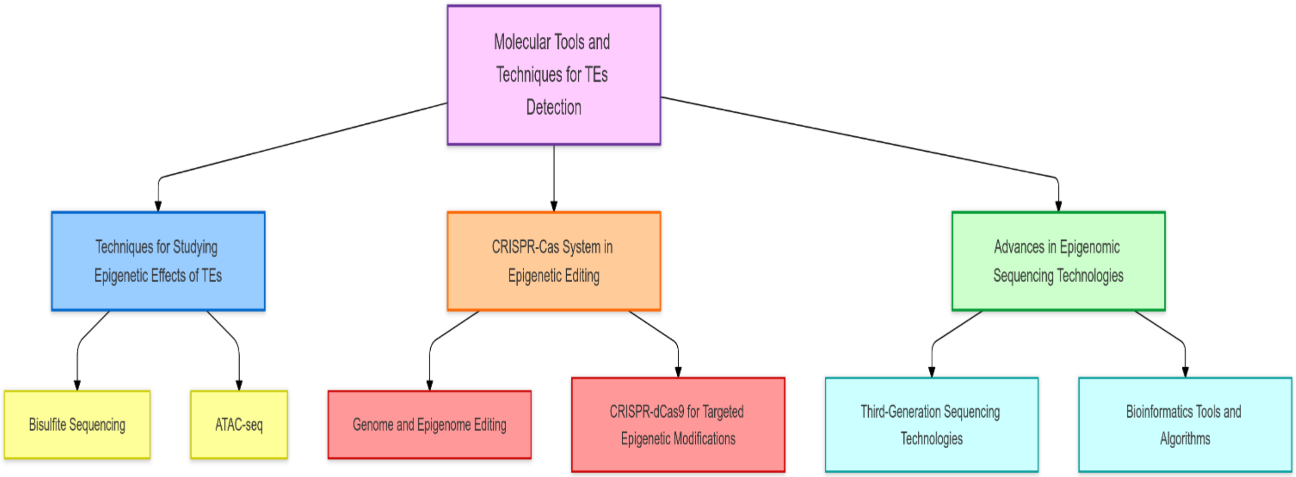

Figure 5. A flowchart diagram illustrating the molecular tools and techniques for Transposable Elements (TEs) detection. This figure shows the various tools and techniques used to detect and study TEs, including PCR-based methods, sequencing technologies, and CRISPR tools. It is closely related to the discussion on advancements in TE research.

Transposable elements in plants: regulatory dynamics and impact on gene expression

Transposable elements (TEs) significantly impact gene expression patterns and genomic integrity, acting as key players in gene regulation and adaptation processes (Galindo-González *et al.*, 2018). Research has shown that TEs can modify the expression of nearby genes by acting as stimulators, silencers, enhancers, or targets of epigenetic modification. This modulation can lead to the creation of mutations, which are often crucial for adaptation to environmental changes. For instance, TEs like the Ac/Ds in peas can result in distinct phenotypic changes, such as the shriveled phenotype, by inserting into genes like the starch branching enzyme SBEI (Fambrini *et al.*, 2020).

Beyond causing mutations, TEs can influence gene expression by disrupting regulatory regions of host genes, both positively and negatively (Hirsch and Springer, 2017). This is evident in various plant species where changes in flowering time and other developmental processes have been linked to TE insertions (Lisch, 2013). For example, inserting MITEs in maize and retrotransposons in the *BrFT2* gene illustrates how TEs can disrupt gene expression (Negi *et al.*, 2016). Similarly, a retrotransposon near the maize tb1 locus leads to increased apical dominance, showcasing the role of TEs in morphological traits (Stitzer *et al.*, 2021).

Maintaining a delicate balance between TE expression and repression is crucial for plant survival and evolution (Galindo-González *et al.*, 2018). This balance ensures that TEs' expression is neither detrimentally high nor insufficiently low (Mhiri *et al.*, 2022). Retrotransposons, which constitute a significant part of many organisms' genomes, modulate this balance by influencing the expression and repression of essential genes (Negi *et al.*, 2016). Interestingly, TEs are not randomly distributed throughout the genome; their insertion locations are often biased, suggesting a strategic placement that aids in maintaining the balance of expression and suppression (Sahebi *et al.*, 2018).

This balance is further maintained by the host's use of various factors, including chromatin structure, DNA modification pathways, siRNA, and sequence-specific repressors like KRAB-ZFPs (Giménez-Orenga and Oltra, 2023). In addition, self-regulatory mechanisms in elements like Mariner-like elements (MLEs) control their amplification and copy number through overproduction inhibition (Ramakrishnan *et al.*, 2021). In reproduction, plants have developed strategies where TEs are only activated in germlines, not somatic cells, indicating a sophisticated regulatory system (Pachamuthu and Borges, 2023).

Furthermore, TE repression is relieved in a homologous cell produced during meiosis in flowering plant species, which does not pass genetic information to the next generation (Vigneau and Borg, 2021). This strategy exemplifies the intricate mechanisms plants have evolved to regulate TE activity, ensuring genomic stability while allowing for necessary genetic variability.

Implications for agriculture

The understanding of transposable element (TE) mechanisms offers significant potential for agricultural improvement. For instance, the manipulation of TEs in rice (*Oryza sativa*) has been used to enhance tolerance to submergence by activating the *Sub1A* gene, a key regulator in the plant's response to flooding (Xu *et al.*, 2006). In maize (*Zea mays*), TEs have been harnessed to improve drought tolerance by modulating genes involved in water use efficiency and root architecture (Makarevitch *et al.*, 2015). Additionally, CRISPR-based targeting of TEs has been employed to alter their activity, leading to changes in gene expression that improve grain yield under stress conditions (Rodríguez-Leal *et al.*, 2017). These examples illustrate how leveraging TE activity can be instrumental in developing crops with enhanced resilience and productivity, which is crucial in the face of climate change and global food security challenges.

Implications for plant growth and development

The function of transposable elements in developmental control

Transposable elements (TEs) play a pivotal role in the regulation of plant development, influencing gene activity and contributing to developmental flexibility and diversity. Their presence and activity within the genome are intricately linked to the developmental stages of plants, acting as key regulatory elements that modulate gene expression in response to developmental cues (Gebrie, 2023; Zhang *et al.*, 2023). Activation of specific TEs during certain growth phases can alter the expression of neighboring genes, leading to variations in plant morphology such as leaf size, flower structure, and root system architecture, which, in turn, affects the plant's ability to adapt to its environment (Rymen *et al.*, 2020).

TEs induce epigenetic modifications, including changes in DNA methylation and histone configurations, that influence gene expression throughout plant development. These epigenetic alterations can be stable and heritable, playing a crucial role in shaping plant growth patterns and traits (Ariel and Manavella, 2021). By introducing new promoters, enhancers, or alternative splicing sites, TEs contribute to the formation of novel gene regulatory networks, facilitating the emergence of new phenotypes and aiding in species diversification (Deneweth *et al.*, 2022).

The insertion of TEs into or near genes can disrupt existing functions or create new ones, enhancing genetic diversity within plant populations. This diversity is vital for plant evolution and adaptation, enabling species to navigate and thrive in changing environmental conditions (Schrader and Schmitz, 2019). Furthermore, TEs can cause genomic rearrangements, leading to the creation of new genes or gene variants—a process that is particularly advantageous in dynamic environments where novel traits may confer a survival benefit (Ramakrishnan *et al.*, 2022).

Stress memory and transgenerational epigenetic inheritance in plants

Transposable elements (TEs), such as the ONSEN retrotransposon in *Arabidopsis* (Roquis *et al.*, 2021) and the Suppressor-mutator (Spm) element in maize (Baduel and Colot, 2021), are central to stress memory and transgenerational epigenetic inheritance in plants. This area is drawing more attention due to its relevance in plant adaptation and evolution (Ramakrishnan *et al.*, 2022). Activated by environmental stressors like heat, drought, or salinity, these elements can cause significant epigenetic changes. These changes impact the stress response of the current generation of plants and can also be inherited by future generations, enhancing their stress resilience (Chang *et al.*, 2020).

The notion of stress memory suggests that a plant's initial exposure to stress leads to genetic and epigenetic alterations, preparing it for more effective responses to similar stress (Sun *et al.*, 2021). An example is the ONSEN retrotransposon in *Arabidopsis* (Nozawa *et al.*, 2022). Upon heat stress exposure, ONSEN becomes active, producing small RNAs targeting genes related to heat stress response (Matsunaga *et al.*, 2015). The resulting changes in gene expression create stable epigenetic marks, which are inherited by the next generation, thereby enhancing their heat tolerance (Roquis *et al.*, 2021). In maize, the Spm element is similarly activated under stress conditions, causing genome-wide changes in DNA methylation patterns and altering the expression of stress-responsive genes (Gill *et al.*, 2021). This TE-driven epigenetic modification under stress is vital for developing stress memory, helping plants respond more efficiently to future stressors (Marin *et al.*, 2020).

Transgenerational epigenetic inheritance refers to the passage of these stress-induced epigenetic changes from generation to generation (Shanker *et al.*, 2020). In various plant species, such as rice with the Tos17 retrotransposon, offspring of stressed plants exhibit altered stress responses without direct exposure to the stressor . This indicates that the stress experiences of parent plants directly affect their offspring's adaptability and survival. The underlying molecular mechanisms of stress memory and transgenerational epigenetic inheritance involve complex interactions between TEs, epigenetic processes, and environmental signals (Gallusci *et al.*, 2023). TEs can trigger epigenetic changes through DNA methylation, histone modification, and the production of noncoding RNAs, altering gene expression to better handle stress . These changes can be stable enough to pass through the germline to offspring. Furthermore, TE activation under stress can lead to genomic rearrangements and the creation of new gene variants, increasing genetic diversity within plant populations . This TE-induced variability is crucial for plant evolution, aiding adaptation to environmental changes.

Ongoing research into TEs' role in stress memory and transgenerational epigenetic inheritance reveals how plants adapt to their environment (Shanker *et al.*, 2020; Baduel and Colot, 2021). It shows that TEs are more than just genomic elements; they actively contribute to plant survival and evolution (Mhiri *et al.*, 2022). They enable rapid adaptation to environmental changes, not just through immediate responses but also by conveying these adaptations to subsequent generations.

Interaction between epigenetic and genetic elements in plants

The complex interaction between epigenetic and genetic elements, driven by transposable elements (TEs) like maize's Activator/Dissociator (Ac/Ds) system , barley's BARE-1 , and rice's Tos17 , plays a crucial role in defining plant genomes and their reaction to environmental factors. Once regarded as mere 'junk DNA', TEs are now recognized for their substantial impact on genetic and epigenetic processes, which are crucial for plant adaptation and evolution . These elements are dynamic within the genome, capable of causing both structural and functional modifications.

TEs such as Ac/Ds in maize and BARE-1 in barley are notable for their genome mobility, leading to genetic variation. Their transposition can cause mutations by disrupting functional genes or changing gene regulatory networks . For example, the Ac/Ds system in maize is well-studied for its mutation-inducing ability, contributing to genetic diversity. These mutations can be advantageous, serving as a basis for natural selection and enabling plants to adapt to environmental shifts. Similarly, BARE-1 in barley is linked to generating genomic diversity, which is essential for plant survival and adaptation.

Beyond their role in genetic diversity, TEs like Tos17 in rice also engage in epigenetic modifications (Cui and Cao, 2014). They can reshape the epigenetic landscape by altering DNA methylation patterns and histone modifications (Galindo-González *et al.*, 2018). The activation or silencing of Tos17 under various stress conditions can lead to DNA methylation changes, influencing gene expression nearby. This epigenetic regulation is vital for plant development and stress response, offering a flexible and reversible method to control gene expression (Ramakrishnan *et al.*, 2021).

The synergy between TE-induced genetic changes and epigenetic modifications forms a complex regulatory network (Mirouze and Vitte, 2014). For example, a TE insertion into a gene or its regulatory area can disrupt its function and attract epigenetic modifications, further affecting gene expression. This interplay is crucial for plant development, integrating environmental signals into the genomic framework and leading to adaptive gene expression changes.

The combined genetic and epigenetic influences of TEs are pivotal in plant development and adaptation (Galindo-González *et al.*, 2018). They allow plants to respond rapidly to environmental alterations, either through new genetic variants via mutations or by modulating gene expression through epigenetic adjustments (Rey *et al.*, 2016). This adaptability is critical for plant survival, enabling them to withstand various stressors like drought, salinity, and temperature changes . TEs also contribute significantly to the long-term evolution of plant species. By inducing genetic and epigenetic variability, they provide material for natural selection, potentially leading to new traits and adaptation to novel environments (Bennetzen and Wang, 2014). The dynamic nature of TEs, along with their responsiveness to environmental cues, positions them as key contributors to the evolutionary narrative of plants (Bousios and Gaut, 2016).

Impact of TEs on plant genome architecture

Transposable elements (TEs) are dynamic entities that modify the dimensions, composition, and capabilities of the plant genome. These are more than simply inactive DNA segments found in the genomes (Baduel *et al.*, 2021). Their activities result in a range of genomic alterations, from small tweaks to large reorganizations, all of which are necessary for plant adaptation and the processes of evolution (Colonna Romano and Fanti, 2022).

One of the most evident effects of TEs on plant genomes is variation in genome size. TEs can make up a significant portion of plant genomic DNA, and as TEs multiply, the genome gets bigger (Stuart, 2018). For instance, TEs play a major role in the genomes of species like maize and wheat, which helps explain the latter's enormous size (Fambrini *et al.*, 2020). The correlation between the genome's size and TE content emphasizes the importance of TEs in the process of genomic expansion by serving as a genomic buffer that may facilitate evolutionary innovations and adaptations (Giménez-Orenga and Oltra, 2023).

Furthermore, TEs are the source of chromosomal rearrangements like translocations, inversions, deletions, and duplications. These rearrangements can lead to phenotypic variability, which can impact gene expression and function (Kremer *et al.*, 2020). For example, transposon migration (TEs) can alter gene sequences or gene regulatory regions, which can impact patterns of gene expression. These rearrangements have been connected to the evolution of novel traits in plants and can help them quickly adapt to changing environmental conditions (Fambrini *et al.*, 2020).

Role of transposable elements in plant stress responses

Systematic analyses across various plant systems have revealed that Transposable Elements (TEs) significantly regulate host gene expression and genomic rearrangement. This involvement of TEs in gene expression control is evident under different environmental conditions, as outlined in studies by Lisch (2013). TEs contribute to the release of cis-regulatory elements, enabling the host genome to manage its genes effectively. This gene regulation manifests in two primary forms: short-term adjustments, adapting to immediate environmental changes, and long-term adjustments, contributing to evolutionary changes, as discussed by Ramakrishnan *et al.* (2021).

The transposition of TEs at the genome level can lead to mutations that create new functional protein-coding sequences, a concept explored by (Chuong *et al.*, 2017; Pisoschi *et al.*, 2021). These mutations often result in environmental adaptation.

For instance, in plants, TEs-induced mutations have been observed to foster adaptation to local environments. In Arabidopsis, this is exemplified through the expression of photoregulation genes associated with FAR1 and FHY3, derived from a mutator-like transposase. The increased gene expression through this protein's direct binding to target genes' promoters suggests Arabidopsis's adaptation to changing light environments, as noted by Lin *et al.* (2007).

In soybeans, phenotypic experiments and allelic distribution analysis demonstrated adaptation to higher latitudes due to the TE insertion in GmphyA2, a paralog of encoding phytochrome A. This was explored by (Liu *et al.*, 2008; Kanazawa *et al.*, 2009). Similarly, various mutations in vernalization genes, essential for changes in growth habits, were induced by TEs in wheat. These mutations have contributed to wheat adaptation to a wide range of environments, as observed by (Yan *et al.*, 2006; Chu *et al.*, 2011).

These findings underscore the pivotal role of TEs in plant stress responses. By inducing mutations and affecting gene expression, TEs enable plants to adapt to their immediate surroundings and evolve, facing various environmental challenges. This dynamic interplay between TEs and plant genomes highlights the complexity and adaptability of plant life, showcasing how genetic mechanisms contribute to the survival and evolution of plant species in diverse ecosystems.

TEs - activation cues under stress

Plants respond to various stress levels, including molecular, tissue, anatomical, and morphological changes. These responses involve alterations in membrane regulation, cell wall structure, transcription, and metabolic processes (Shinozaki *et al.*, 2003; Hirayama and Shinozaki, 2010). Research indicates that under biotic and abiotic stress, Transposable Elements (TEs) are expressed and activated through translocation. Stress often activates TEs by reducing their inactive epigenetic state or through Transcription Factors (TFs) (Sun *et al.*, 2020). Activated TEs under stress can alter gene expression near their insertion sites, leading to phenotypic adaptability (Negi *et al.*, 2016; Chuong *et al.*, 2017; Dubin *et al.*, 2018). However, some studies also report TE suppression or harmful effects of TE activation under stress, highlighting a complex TE-stress relationship (Sun *et al.*, 2020). Specific TE sequences linked to stress response, such as LTR retrotransposons with cis-regulatory elements in their 5' LTR, have been identified, triggering transposon activation under stress (Kumar and Bennetzen, 1999).

Transposon transcription under environmental stress involves two mechanisms. The first involves specific TFs interacting with the transposon promoter sequence. In plant retrotransposons, DNA elements related to stress response signals, like plant hormones, are found in the 5'LTR (Casacuberta and González, 2013). These elements act as crucial motifs for gene activation under stress. For example, in Arabidopsis, the ONSEN LTR retrotransposon is activated by heat stress factors recognizing a sequence in its promoter (Ito *et al.*, 2011; Cavrak *et al.*, 2014). ONSEN transcription is triggered at 37°C (Ito *et al.*, 2011), with the heat shock factor binding to the heat shock element in the LTR 5' ONSEN (Cavrak *et al.*, 2014). Another study on Arabidopsis showed ONSEN's insertion site preference related to specific chromatin states, particularly those rich in histone H2A.Z and H3K27me3 (Roquis *et al.*, 2021). In rdd-regulated stress response promoters, short TE sequences and their demethylation confer resistance against *Fusarium oxysporum* (Le *et al.*, 2014). In *A. lyrata* and *A. thaliana*, heat-responsive TEs like ONSEN, COPIA37, TERESTRA, and ROMANIAT5 were identified, with COPIA families in seven Brassicaceae species showing heat-responsiveness due to HSF-binding HREs in their long terminal repeats (Pietzenuk *et al.*, 2016). In tomatoes, the Rider Copia retrotransposon is expressed under drought stress and abscisic acid signaling, containing dehydration-responsive elements in its promoter (Benoit *et al.*, 2019).

TE insertion in regulatory regions can induce stress-related gene expression. In corn, MITE 82 insertion in the ZmNAC111 promoter led to gene expression repression, with ZmNAC111 overexpression enhancing drought stress tolerance and water use efficiency through H3K9 demethylation (Mao *et al.*, 2015). In rice, the GSTL2 promoter contains two transposons, affecting expression while being balanced by enhancer elements (Hu et al., 2011).

Another mechanism involves reactivating suppressed transposon sequences under stress, as environmental stress alters epigenetic modifications and gene expression patterns, including transposons (Kumar *et al.*, 2013). In rice, many LTR-retrotransposons were up-regulated under iron stress, with 156 out of 369 families expressed (Finatto *et al.*, 2015). Maize, with its diverse TE types, shows TE-regulated gene expression under various stresses (Makarevitch *et al.*, 2015). In *Antirrhinum majus*, the Tam3 DNA transposon, inactive at high temperatures, activates at low temperatures, and is linked to DNA methylation changes (Kitamura 2001). Arabidopsis experiences reduced chromosomal interactions under heat stress, correlating with TE activation (Sun *et al.*, 2020). In rice, new mPing MITE insertions up-regulate adjacent genes under low temperature or salinity, with no expression change in control conditions (Naito *et al.*, 2009; Yasuda *et al.*, 2013). Figure 6 presents examples of TE activation under stress.

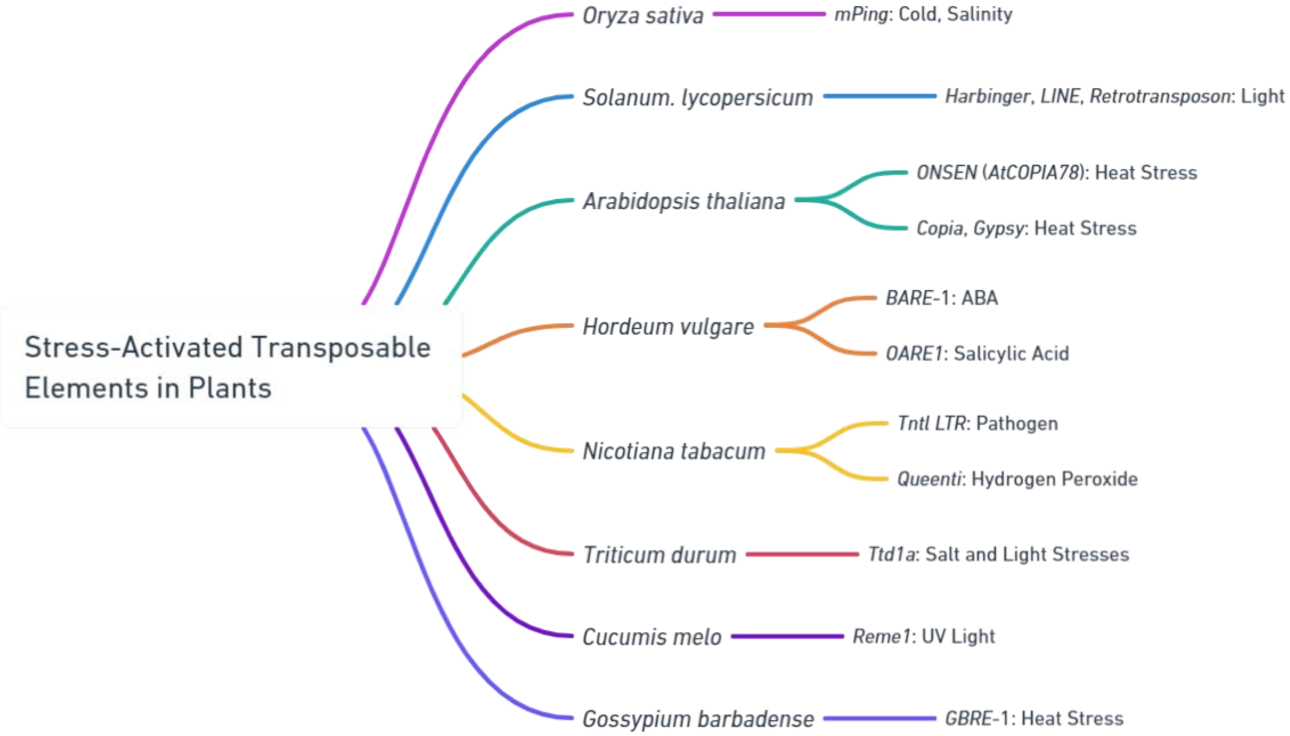

Figure 6. Examples of stress-activated TEs in some plants. This figure presents specific examples of TEs that are activated under stress conditions in different plant species, providing quantitative data to support the discussion on stress-induced TE activation and its adaptive significance.

According to the studies that have been conducted, it has been stated that TEs in plants may induce the reaction of adjacent genes via providing stress-responsive enhancer functions and activation of TEs under stress conditions affiliated with factors such as stress type, TEs type, its genomic location, and the genetic background of the host (Figure 7) (Deneweth *et al.*, 2022).

Activation of TEs does not always occur under stress conditions, but stress activates and suppresses TEs depending on the context. For example, transposable elements' response to high temperature was investigated in several ecotypes of *Arabidopsis thaliana*, the results showed that in 7 ecotypes, most TEs had a higher expression under stress. In comparison, in the other 3 ecotypes, most transposable elements had lower expression levels under stress conditions (Barah *et al.*, 2013; Horváth *et al.*, 2017), which indicates that the suppression of TEs may also occur in the stress condition. Excessive iron stress altered the transcription of 37% of LTR-retrotransposon, suggesting that the expression level of 95.4% increased and about 4.6% showed a decrease in expression (Finatto *et al.*, 2015).

Stress regulation by Te-lncRNAs

Long noncoding RNAs (lncRNAs), a subgroup of RNAs, play a crucial role in regulating gene expression and key cellular activities, including reactions to phosphate and sulfur deprivation, as well as salt stress. These RNAs, characterized by lengths exceeding 200 nucleotides, cannot code for proteins. In Arabidopsis, numerous lncRNAs exhibit significant reactions to stressors like drought, cold, high salt levels, and abscisic acid (Di *et al.*, 2014; Qin *et al.*, 2017; Zhao *et al.*, 2018). *Arabidopsis thaliana* has a notably higher count of TE-containing lincRNAs (Te-lincRNAs) than *Zea mays* and *Oryza sativa*, correlating with the number of transposable elements (TEs) in their genomes. Certain Te-lincRNAs play a role in stress response. Research on Arabidopsis revealed that lincRNAs are crucial in abiotic stress response, with Arabidopsis thaliana mutants in Te-lincRNA11195 displaying enhanced resistance to ABA treatment compared to wild types (Wang *et al.*, 2017). In maize, 65% of 23,309 identified lncRNAs showed sequence similarity to transposable elements, predominantly retrotransposons with long terminal repeats from the *Copia* and *Gypsy* superfamilies, with over 1077 reacting to abiotic stress (Lv *et al.*, 2019). Studies on *Solanum lycopersicum* and *S. pennellii* showed that Lycopersicon-specific lncRNA sites originate from TEs (Wang *et al.*, 2016).

Stress regulation by Te-siRNA

Epigenetic mechanisms play a crucial role in silencing and deactivating most transposable elements (TEs) in plant genomes, with the epigenetic activity of TEs influencing the host plant's stress response (Lippman *et al.*, 2003; McCue *et al.*, 2012). DNA methylation is a critical factor in controlling transposon expression. In Arabidopsis, Attila LTR retrotransposons, which form the largest TE family, are transcriptionally silenced through symmetric CG DNA methylation. This silencing can be reversed by reducing or removing DNA methylation, leading to transcriptional activation (Wright and Voytas, 1998; Steimer *et al.*, 2000). In DNA hypomethylation mutants, activation of TEs is observed (Mirouze *et al.*, 2009; Tsukahara *et al.*, 2009). Methylation acts as a defense mechanism, preventing excessive TE activation and protecting against abnormal transposon activity. RNA-directed DNA methylation (RdDM) is another method for regulating TEs, using siRNA-mediated DNA methylation to control them (Wierzbicki *et al.*, 2008; Gao *et al.*, 2010).

Gene expression is also regulated by suppressing TE activity through small RNAs. Research on *Arabidopsis thaliana* indicates that the production of TE-associated endogenous small interfering RNAs (Te-siRNAs) differs from other gene-regulatory small RNAs (sRNAs), such as microRNAs or trans-acting siRNAs (McCue *et al.*, 2012).

TEs are known to activate under biotic and abiotic stresses, impacting the expression of stress-related genes. A study on the *Ty1/copia* retrotransposon ONSEN, activated by heat stress in Arabidopsis, revealed that siRNA pathways regulate ONSEN's transcriptional activation (Matsunaga *et al.*, 2015). DNA demethylases like ROS1, DML2, and DML3 play roles in fungal disease resistance in Arabidopsis by maintaining or enhancing the expression of stress response genes necessary for combating *Fusarium oxysporum*. An rdd triple mutant of DNA demethylase (ros1 dml2 dml3) showed increased susceptibility to this pathogen (Le *et al.*, 2014). Furthermore, a study on *A. thaliana* under phosphate starvation showed that a cluster of sRNAs (smRPi1LTR) derived from the Copia95 LTR retrotransposon indicates TE-mediated regulation of plant stress response gene expression through small noncoding RNAs derived from TEs during stress (Hsieh et al., 2009).

Future directions and challenges in TE research

The field of transposable element (TE) research stands at a dynamic juncture, propelled by technological advancements and deepening theoretical insights. However, it also faces significant challenges that must be addressed to unravel the complexities of TEs and their roles in genomes (Figure 8). Recent years have seen remarkable progress in sequencing technologies and bioinformatics tools, offering unprecedented opportunities to study TEs (Omony *et al.*, 2020). Long-read sequencing technologies, such as nanopore and single-molecule real-time (SMRT) sequencing, have begun to overcome the limitations of short-read sequencing in resolving repetitive TE sequences (Kulski, 2016; Usha *et al.*, 2022). Furthermore, the application of CRISPR-Cas systems for precise editing and epigenetic modification of TEs opens new avenues for functional studies (Saika *et al.*, 2019; Merkulov *et al.*, 2023). Looking forward, the integration of these technologies with advanced computational models and machine learning algorithms promises to enhance our ability to identify, annotate, and understand the functional dynamics of TEs in various genomes.

The conceptual frameworks guiding TE research are evolving. There is a growing recognition of the need to view TEs not just as isolated genetic elements but as integral components of complex regulatory networks within the genome (Bennetzen and Wang, 2014). This perspective necessitates a holistic approach to studying TEs, combining genomics, epigenetics, systems biology, and evolutionary biology (Galindo-González *et al.*, 2018). Future research will likely focus on elucidating the systemic effects of TEs, including their impact on gene regulatory networks, chromatin architecture, and genome evolution.

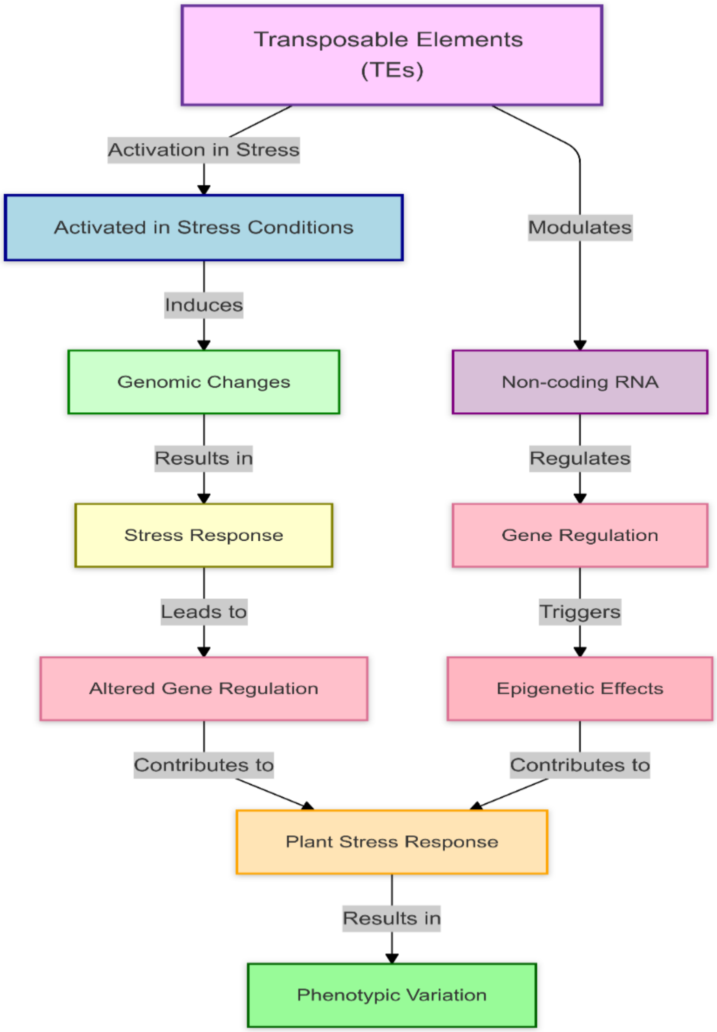

Figure 7 A flowchart diagram illustrating the role of Transposable Elements (TEs) in plant stress response. This figure shows the interplay between TE activation and silencing under stress conditions, highlighting their contribution to the plant's ability to adapt to environmental challenges.

Despite these advancements, TE research faces several challenges. One of the primary obstacles is the accurate annotation and characterization of TEs in genome sequences. The repetitive and diverse nature of TEs makes them difficult to identify accurately, requiring the development of more sophisticated computational tools and algorithms (Platt *et al.*, 2016). Another challenge lies in deciphering the complex regulatory roles of TEs, particularly their interactions with host genomes and their influence on gene expression and epigenetic states. Additionally, understanding the evolutionary dynamics of TEs and their contributions to genetic diversity and adaptation remains a daunting task (Viviani *et al.*, 2021).

Addressing these challenges will require concerted efforts across multiple disciplines. Improvements in sequencing technology and bioinformatics are essential for better TE annotation and characterization. Functional studies of TEs will benefit from innovative genetic and epigenetic editing techniques, allowing for the dissection of their regulatory roles. Moreover, collaborative research initiatives that bring together experts from genetics, epigenetics, computational biology, and evolutionary biology can accelerate the generation of comprehensive models of TE activity and function.

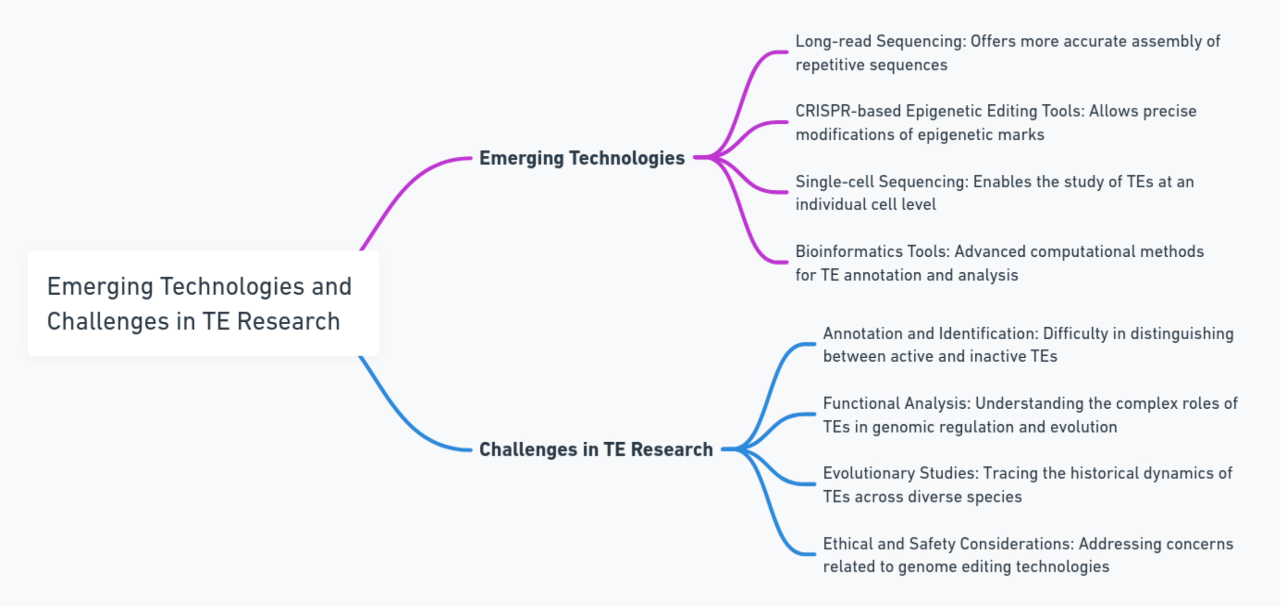

Figure 8. Emerging technologies and challenges in TE research. This figure summarizes the latest technological advancements in TE research, such as CRISPR-based tools, and discusses the challenges that researchers face. It aligns with the discussion on the future directions of TE studies and their implications for plant breeding.

Ethical and ecological considerations

While the application of TE-based biotechnologies holds immense promise, it also raises several ethical and ecological concerns. Manipulating TEs could lead to unintended off-target effects, potentially disrupting non-target genes and causing deleterious traits. Ecologically, the activation of TEs might introduce novel genetic variations that could impact biodiversity, especially if engineered plants crossbreed with wild relatives. Furthermore, the long-term consequences of altering TE dynamics on genome stability are not fully understood, necessitating careful assessment and regulation. Ethical considerations include public acceptance of genetic modifications, especially those involving elements with potential mobility, which may evoke concerns about the safety of such technologies. Therefore, responsible research, rigorous regulatory frameworks, and transparent public communication are essential for the sustainable application of TE-based innovations in agriculture (Howell *et al.*, 2018).

Conclusion

Transposable elements (TEs), once overlooked as 'junk DNA,' have emerged as fundamental components of plant genomes, playing a pivotal role in their adaptation to environmental stresses. Particularly, retrotransposons, residing within both heterochromatin and euchromatin regions of chromosomes, underscore their functional significance in genomic structure and activity. Their strategic distribution across the genome facilitates vital processes such as gene regulation, creation of new genes, and genetic recombination, contributing to plant diversity and evolutionary adaptability.Our review underscored the dynamic role of TEs, especially retrotransposons, in modulating gene expression in response to environmental changes. By either up-regulating or down-regulating adjacent genes, TEs serve as key regulators of plant stress responses, enabling resilience against various abiotic and biotic stressors. The production of transposon-derived small interfering RNAs (Te-siRNAs) and long intergenic noncoding RNAs (TE-lincRNAs) further exemplifies their intricate role in gene expression regulation and epigenetic silencing, highlighting the complex interplay between TEs and plant stress mechanisms.

Despite significant advancements in understanding the relationship between TEs and plant stress responses, several areas warrant further exploration. Future research should aim to delineate the precise molecular pathways through which TEs influence neighboring gene expression under stress conditions. Investigating the role of TEs in a broader spectrum of plant species will enrich our comprehension of their universal and species-specific impacts on stress adaptation.

The practical applications of our expanding knowledge of TEs are vast, especially in the fields of agriculture and biotechnology. Understanding the mechanisms by which TEs contribute to stress resilience offers promising avenues for the development of climate-resilient crop varieties. By harnessing the natural genetic diversity and regulatory capabilities of TEs, we can engineer crops that are better equipped to withstand environmental challenges, thus ensuring food security in the face of changing global climates.

In conclusion, TEs are not mere genomic relics but are dynamic and integral to plant stress responses and evolution. Their study not only reveals the complexity of plant genomes but also opens up new frontiers in agriculture and biotechnology, where their potential can be harnessed for sustainable and resilient crop production. Looking ahead, advancements in sequencing technologies, coupled with the development of precise genome-editing tools such as CRISPR, hold promise for uncovering novel functions of TEs and their regulatory networks. Future breakthroughs may involve the targeted activation or silencing of specific TEs to enhance desirable traits in crops, such as increased tolerance to extreme temperatures or improved nutrient efficiency. Moreover, addressing the ecological and evolutionary implications of manipulating TEs will be crucial for safely implementing these technologies. The integration of interdisciplinary approaches will be key to unraveling the full potential of TEs in plant adaptation, paving the way for innovative solutions to agricultural challenges in the face of climate change.

Supplementary Materials

No supplementary material is available for this article.

Author Contributions

MN, MK and AKGS developed the concept, performed the database search, partially collected the data, analyzed, interpreted the results and finalized the draft. PS revised the manuscript. MK and PS supervised this study. All authors approved the final version of the manuscript.

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Conflict of Interest Statement

The author declares no conflict of interest.

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عناصر جابه‌جاشونده: بینشی مکانیکی به چشم‌انداز تنظیم‌کننده پویا از پاسخ به تنش‌ها در گیاهان (با تکیه بر مفاهیم کشاورزی)

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چکیده: عناصر ژنتیکی جابه‌جاشونده (TEs) توالی‌های DNA پویایی هستند که به‌طور قابل‌توجه بر بیان ژن در گیاهان تأثیر می‌گذارند و امکان سازگاری با تنش‌های محیطی را فراهم می‌کنند. این بررسی نقش TEها را در سازگاری گیاه، با تمرکز بر مکانیسم‌های فعال‌سازی و سرکوب TE، از جمله بازسازی کروماتین، تغییرات DNA، و RNAهای مداخله‌کننده کوچک (siRNA) بررسی می‌کند. شرایط تنش‌زا از طریق تعامل بین فاکتورهای رونویسی ناشی از تنش و محرک های TE باعث فعال شدن TE می‌شود، همانطور که در خانواده‌های رتروترانسپوزون مانند COPIA93 و ONSEN در تعدیل ژن‌های پاسخگو به تنش دیده می‌شود. درک این مکانیسم‌ها بینش ارزشمندی را برای کشاورزی، به‌ویژه در توسعه گیاهانی که در برابر تغییرات آب و هوایی مقاوم هستند، ارائه می دهد. استفاده از تنظیم ژن با واسطه TE، استراتژی‌های نوآورانه‌ای را برای افزایش سازگاری گیاه ارائه می‌کند و پتانسیل TEs را در دستکاری ژنتیکی برای به‌نژادی گیاهی برجسته می‌کند.

کلمات کلیدی: عناصر جابه‌جاشونده، تنظیم اپی‌ژنتیکی، سازگاری محیطی، RNAهای غیرکدکننده، تنش گیاهی.

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