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Transposons Activity in Microbial Genomes

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ABSTRACT

A subset of human diseases originates from host genomic sequences, specifically through the involvement of transposons in chromosomal recombination and gene regulation. Transposons act as intrinsic modulators of genome architecture, functioning as remodelers and insertion vectors that may serve as regulatory DNA, functional RNA, or, in certain cases, proteins. Structural variability among transposons drives rapid increases in their abundance and contributes to genome expansion within relatively short evolutionary and adaptive timescales. These elements are highly conserved across distantly related taxonomic groups. Initially regarded as "junk DNA," transposons are now understood to be fundamental elements of genomic construction, contributing to both structural organization and regulatory complexity. Furthermore, CRISPR-associated transposons represent promising molecular tools, enabling RNA-guided integration of large transgenes with significant potential for biotechnological applications.

Keywords: *Silence genes, single and dual system, crawler transposable element, open reading frame.*

Introduction

Mobile Genetic Elements in Microorganisms

Mobile genetic elements (MGEs) such as transposons, introns, integrins, plasmids, and insertion sequences are broadly distributed throughout bacterial and fungal genomes (1). Transposable elements (TEs), commonly referred to as transposons, are especially remarkable because of their capacity to shift positions within genomes, thereby fostering genetic variation and adaptation. Transposable elements are found across diverse organisms, including edible mycorrhizal mushrooms, pathogenic fungi, and yeast, as well as in bacteria such as *Escherichia coli, Bacillus subtilis*, *Lactococcus lactis*, Corynebacterium *glutamicum*, *Klebsiella pneumoniae*, and *Zymomonas mobilis*.; however, their advantageous applications in fungi remain relatively restricted. Introns, which are noncoding DNA segments situated between exons and removed during RNA processing, contrast with transposons that have infiltrated all domains of life as intragenomic parasitic DNA capable of movement ,for instance, Alu elements in primates and Ty elements in yeast (2). Plasmids serve as vehicles for transferring genetic material between genomes, particularly in bacterial cells. Because TEs can shift randomly between plasmids and chromosomes, they may generate insertions, deletions, or duplications; in addition, they enable genetic exchange between chromosomes within the same cell and can encode toxins, drug-resistance enzymes, or diverse metabolic enzymes (3). The relocation process is catalyzed by transposases, which bind to transposon terminals and mediate their movement (4). The involvement of transposons in the development of industrial strains remains poorly understood (5), largely because TEs exert strong influence on gene activation or repression.

Types of Transposable Elements

Transposons are categorized into class I and class II according to their transposition mechanisms; however, the influence of these elements on epigenetic regulation is often overlooked in classical population genetic models, despite their precise contribution to estimating effective population size, identifying specific genetic loci, and revealing structural variations (6). Transposon classes are further subdivided into distinct orders, subclasses, and super families according to their replication strategies, sequence homologies, and structural relationships. Class I transposons, also known as retro elements, operate through a copy-and-paste mechanism (7(in which a DNA segment is first transcribed into RNA and subsequently reverse-transcribed into DNA by the enzyme reverse transcriptase (8(. These elements do not encode transposase enzymes. The three principal orders of retrotransposons include long terminal repeat (LTR) elements, LINE-like (long interspersed nuclear elements), and SINE-like (short interspersed nuclear elements). LINEs and SINEs are particularly abundant in humans and other primates, where they regulate gene expression through modulation of chromatin structure (9, 10, and 11) transcriptional activity, pre-mRNA processing, and other aspects of mRNA metabolism. Their accumulation has contributed substantially to the repetitive content of eukaryotic genomes, and these short retro transposons play critical roles in evolutionary processes. Miniature Inverted-Repeat Transposable Elements (MITEs), as an_example of non-autonomous retrotransposons lack self-reliant,mobility and require external element for amplification. MITEs are classified as non-autonomous members of class II DNA transposons (12).

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The SINE family typically ranges in length from 85 to 500 bp, with examples including Ty elements in yeast (13). Class II transposons or DNA transposons, rely exclusively on DNA molecules and transpose via a cut-and-paste mechanism mediated by transposase (14). They are subdivided into Tc1/Mariner, hAT-like, and Mutator-like super families (14,15) besides other_groups such as Merlin, Transib, P elements, PiggyBac, PIF/Harbinger, CACTA, Crypton, Helitron, Maverick, Sola, and Zator (16,17). Members of the hAT family, containing the maize Activator (Ac), have been systematic over various eukaryotic species (18). This class II type is present in both plants and animals but (19,20)has not been detected in fungal organisms (20,21).Transposons of both class I and class II have been detected in *Aspergillus* species; nevertheless, active transposition has been documented only for class II elements, including Antr1 (22), Tan1 (23), and Vader in A. niger (24). The resident niaD gene, situated at the niaD locus and responsible for coding nitrate reductase, has been utilized as a transposon trap in *A. nidulans*, although its activity is suppressed in the presence of external ammonium (25). *In A. fumigatus*, the Fot1/Pogo-type transposon Aft1 demonstrated transposition activity under elevated temperature conditions (14). Genome sequencing of A. oryzae RIB40 revealed several retro transposons and a DNA transposon (26). Although transcription was detected, transposition activity could not be confirmed through trapping experiments. *Further analysis of industrial A. oryzae* strains identified a new active DNA transposon within the OSI1013 strain, which is utilized in sake fermentation. This element inserted into the niaD gene through spontaneous transposition (27). Named Crawler, it represents a distinct class II DNA transposon that occurs in multiple copies in the industrial strain *A. oryzae* OSI1013 (25).Another active transposon, Restless, was identified in the hyphomycete *T. Inflatum*. Restless is classified as a hAT transposon within the Tc1/Mariner superfamily. It measures 4,097 base pairs in length, features 20-bp inverted repeats along with an 8-bp target site duplication, and encodes a long open reading frame that is interrupted by a single noncoding intron (28, 25)

Alternative splicing of the mRNA generates two distinct transcripts, potentially encoding polypeptides of 157 or 803 amino acids (20). Hybridization assays employing rare-cutting restriction endonucleases verified the presence of roughly 15 copies in *T. inflatum* (20). The observed genomic distribution, transcriptional activity, splicing variation, and mobility of Restless indicate its promise for use in transposon tagging approaches in filamentous fungi. The predicted amino acid sequence of the larger polypeptide exhibits strong similarity to hAT family transposases (20, 28, 29). Chromosomal profiling through pulsed-field gel electrophoresis revealed that each of the seven chromosomal bands contains copies of the 4.1-kb transposon (30).

A newly discovered class II transposon belonging to the Tc1/Mariner superfamily was detected in A. fumigatus. Its potential utility was assessed by comparison with Aft1, a Fot1/Pogo-type transposon from the same superfamily, which has previously been applied in phylogenetic studies (14, 31).

Autonomous vs Non-Autonomous Transposons

The ability of transposable elements to mobilize depends on whether they encode the enzymes required for their own transposition, and in most cases non-autonomous elements, which possess highly degenerate coding regions, lack these enzymes and therefore do not exhibit intrinsic mobility (10). Because they do not contain the genetic information necessary to synthesize the required enzymes, their movement relies on the presence and activity of a functional autonomous transposon within the same genome. For instance, most transposable elements (TEs) identified in *Paracoccidioide*s genomes are non-autonomous and occur in high copy numbers. This abundance renders them stable molecular markers and suitable candidates for species identification within the genus. Non-autonomous TEs, along with remnant copies, are evenly distributed across the genome. An autonomous impala transposon, originally derived from *F. oxysporum* (32, 33), can be engineered to carry selectable markers such as antibiotic resistance genes, thereby facilitating the detection of successful transposition events. Moreover, impala elements have been introduced into the genome of another fungus*, P. griseoroseum* (34). Similarly, Vader, a non-autonomous DNA transposon identified in A. niger, is activated by the transposase encoded by the tan1 gene. This element has been employed in mutagenesis and in the development of novel fungal strains with advantageous traits for biotechnological applications (35).

Composite transposons

These elements represent subsets of non-autonomous transposons and are composed of two inverted repeats derived from separate transposons that move together as a single unit, carrying the intervening DNA. Their mobility depends on transposition machinery encoded elsewhere; typically within flanking insertion sequence (IS) elementsFor instance, Tn10 and Tn5 employ a non-replicative cut-and-paste mode of transposition (36) and when their transposase gene is disrupted or removed they behave as non-autonomous elements, whereas intact transposase expression allows them to retain autonomous mobility.The transposase protein identifies the terminal sequences of the element and excises it from its original location, after which the resulting protein–DNA complex diffuses away from the donor site until random collisions bring it into contact with a new target In order to complete the reaction, the 50-kDa transposase must first cleave four DNA strands to liberate the transposon from its donor locus and then carry out two strand-exchange reactions that enable insertion of the element into the new target site (36).

Non composite Tn3 Autonomous Transposons

It is a widespread family of transposons comprises gene clusters flanked by terminal inverted repeat (IR) sequences. These elements were initially identified as bacterial transposons and are well known for their role in the dissemination of antibiotic resistance (37). In contrast, Ty elements represent yeast-specific autonomous non-composite transposons. Within bacteria, the Tn3 group includes both autonomous and non-autonomous members. The Tn3 transposon is approximately 5.9 kb in length and contains two directly repeated terminal sequences, referred to as long terminal repeats (LTRs) or deltas. Each delta harbors a promoter, protein binding sites that regulate gene activation or repression, and sequences specifically recognized by transposases (38).

Mechanism of DNA Transposition

Transposition occurs through two principal mechanisms: replicative or conservative. In replicative transposition, two daughter copies of the original transposable element are generated, with one copy retained at the parental locus and the other integrated at the target site (16).

In contrast, conservative transposition does not involve replication; instead, the element is excised and relocated to a new genomic site. Transposons can alter their genomic position through four distinct mechanisms (39). In one such process, excision is mediated by the transposase enzyme, which binds to the inverted repeats at the transposon termini and cleaves the element from its original locus. The excised transposon is subsequently inserted into a new genomic location, typically flanked by direct repeats, followed by ligation. DNA gaps generated during this process are repaired via Watson–Crick base pairing, resulting in stable integration. These events contribute to genome expansion, structural rearrangement, adaptation, and evolutionary innovation.

Bioinformatics tools for TE analyses

NCBI, the National Center for Biotechnology Information, hosts an extensive database of DNA and RNA sequences together with the proteins they encode (40). Among its most recognized resources is GenBank, a nucleotide sequence archive that, together with the sequence analysis tool BLAST, facilitates the identification of gene family members. Genomic and transcriptomic analyses, encompassing all RNA molecules expressed within organism, provide critical insights into the regulation of gene activity, illustrating how individual genes are switched on or off within cells. Internal transcribed spacer2 (ITS2) and 18S ribosomal RNA (18SRNA) sequencing represent key molecular techniques for the identification and classification of fungi and yeast. These marker genes are widely employed in molecular biology, as sequencing of specific genomic regions provides valuable insights into fungal taxonomy, phylogeny, and community structure. Whole-genome sequencing (WGS) has further emerged as an essential approach for investigating genetic variation and population structure at a comprehensive scale (20). In contemporary genomics, numerous computational tools are available for the analysis, prediction, and detection of repetitive DNA sequences. Some of the first genome visualization tools were linear browsers, including the UCSC Genome Browser and the Ensemble Genome Browser, which display genomic information through graphical interfaces (41). These platforms support widely used data formats, including FASTA, BED, and GFF, thereby enabling efficient visualization and interpretation of complex genomic datasets.RepeatMasker is widely used to identify, classify, and mask repetitive DNA elements, including low-complexity sequences and interspersed repeats (42). In addition, bioinformatics platforms developed for genomic analysis provide annotation and classification of transposable elements, thereby facilitating their systematic detection (43) tools designed for genomic analysis also annotate and classify transposable elements (TEs), thereby facilitating their detection (44). Commonly used programs include RepeatMasker, RepeatModeler, LTRharvest, and RTAnalyzer. RepeatMasker utilizes a comprehensive database of repetitive DNA elements, aligning input genome sequences against libraries of known repeats. In addition, several programming libraries have been developed to support the creation of custom visualizations. Repbase, for example, serves as a curated reference database of repetitive DNA elements (45). Collectively, these tools enable researchers to visualize and interpret genomic data, though each emphasizes different aspects and employs distinct formats. Complementary visualization platforms such as ModDotPlot and StainedGlass provide rapid, interactive exploration of tandem repeats. Together with RepeatMasker, RepeatModeler, LTRharvest, and RT Analyzer, they form an integrated toolkit for discovering, annotating, and classifying repetitive elements. ModDotPlot and StainedGlass, in particular, specialize in graphical representation of repeat structure and identity. Tandem repeats, defined as sequences occurring directly adjacent to themselves multiple times, can be effectively visualized using ModDotPlot. This tool accepts FASTA-formatted sequences as input and generates self-identity heat maps for each sequence, as well as comparative heat maps for all pairwise combinations.At the population scale, mapping transposable element diversity has indeed been shown to reveal critical connections to gene regulation and epigenomic variation (46). These visualization tools are specifically designed for repeat-rich genomic regions rather than conserved marker genes.

Application of Transposons

Transposons represent valuable diagnostic tools in molecular biology owing to their intrinsic capacity to mobilize and integrate into the genomes of diverse organisms. So, they are capable of introducing foreign DNA sequence (47, 48), they can function as selectable markers, transformation vectors, cloning vehicles, and therapeutic constructs within target cells. Through these roles, transposons facilitate genome manipulation, regulate gene expression, and contribute to genetic variability. Their activity can also induce morphological changes and promote adaptation to environmental conditions, thereby underscoring their importance in both fundamental research and applied biotechnology (4).

Transposon Mutagenesis and Functional Genomics

Although chemical or physical approaches to random mutagenesis are relatively simple to apply, pinpointing the exact mutation sites within microbial genomes is often challenging. By comparison, transposon insertion mutagenesis offers a more effective strategy for targeted gene disruption and the modification of phenotypes (49). This approach is user-friendly, cost-effective, traceable, and exhibits minimal bias toward specific loci, despite the diverse defense mechanisms that fungi have evolved against transposable elements (TEs) (17). Organisms have developed multiple molecular strategies to regulate and suppress transposons. Among these are genome defense systems mediated by CRISPR-Cas complexes, which function as adaptive immune mechanisms in bacteria and archaea (12, 50).

In fungal systems, a unique defense mechanism termed repeat-induced point (RIP) mutation acts on duplicated DNA sequences, especially transposable elements, thereby limiting their spread and reducing their possible pathogenic consequences (30,5,15 ,253(Transposon mutagenesis, once established, can generate a large pool of mutants (50(. During repeat-induced point (RIP) mutation (55), duplicated DNA sequences undergo efficient and irreversible C:G to T:A transitions, which block transposon replication. This repeat-induced point (RIP) process has been documented in transposable elements of *Aspergillus* niger and *Penicillium chrysogenum*. *In P. chrysogenum*, RIP has impacted a wide range of sequences, many of which also carry additional mutations (55, 56, 57).

In Aspergillus niger, RIP activity is confined to a limited number of sequences, though nearly all mutations exhibit RIP-like features (57, 58).

Interestingly, RIP in *A. niger* is observed solely within transposon sequences that contain disrupted open reading frames, a phenomenon not yet described in other fungal species (29, 57) In both fungi examined, two sequences were identified that share strong similarity to the *Neurospora crassa* RID gene. RID, considered a putative DNA methyltransferase, remains the only enzyme known to participate in the RIP pathway and contributes more broadly to the preservation of genome integrity (11).

A study shows that the polar psychrotrophic fungus *Geomyces sp* (58) produces geomycamine, a high-quality natural red pigment. Researchers used transposon insertion mutagenesis to generate mutants capable of producing pigment at normal temperatures with potential applications as an edible pigment (59,60) ,overcoming the limitation of low-temperature dependence for industrial applications. Both Minos and Restless transposons are utilized in genetic mutagenesis.The Minos element, a DNA transposon classified within the Tc1/Mariner superfamily, was originally isolated from Drosophila hydei and demonstrates broad activity in this species (61).Its transposition frequency is comparable to that of impala as the latter represents a well-recognized instrument for functional gene analysis in fungi. The Minos transposon integrates at random throughout the host genome, showing only a minor bias toward TA dinucleotides (61, 62), and generates a characteristic 6-bp footprint upon excision (61.63). Furthermore, the first fungal hAT transposon, termed Restless, was identified in Tolypocladium inflatum (55, 61) Restless generates an 8-bp target site duplication upon integration and has been demonstrated to retain excision and integration activity in heterologous hosts such as *Neurospora crassa* and *Penicillium chrysogenum* (61). Both Minos and Restless are "cut-and-paste" DNA transposons, capable of excising a defined cassette or sequence from the donor locus and inserting it randomly into new genomic sites (63). Nevertheless, the degree of randomness in the excision and insertion of Minos and Restless within Geomyces sp. WNF-15A remains unresolved (63). Dual systems that combine Minos and Restless have demonstrated greater efficiency than single systems in fungal mutagenesis, although the proportion of positive mutations is comparable between dual and single transposon approaches (63). These transposons serve as alternative tools for genetic mutagenesis and strain development in fungi from extreme environments as it is the case in cold-adaptive genes (64).Their activity can modulate gene expression either by disrupting open reading frames or by integrating near protein-coding genes (16, 65).

Transposon Tagging and Epigenetic Impact

Transposon tagging consists of triggering transposition, examining mutations that arise from transposon insertions, determining the specific element accountable for the mutation, and ultimately cloning the gene that has been tagged (66) . Four principal strategies are employed for gene tagging: marker-based tagging, transposon tagging, DNA tagging, and epitope tagging.

Within fungal epigenetics, transposable elements (TEs) are subject to regulation through epigenetic marks, including DNA methylation, histone acetylation, and distinct histone modifications (11). Epigenetic marks can spread into neighboring genes, leading to changes in gene expression without altering the DNA sequence itself. These modifications are typically maintained through successive cell divisions, though they remain responsive to environmental influences.

DNA methylation patterns exhibit strong tissue specificity and are essential for controlling gene activity across diverse cell types and developmental stages (67). Because TEs can insert randomly into genomes, DNA methylation serves as a natural biochemical mechanism to silence or inactivate transposons (68).

In microbial communities, tagging particular strains frequently relies on selectable and/or optical marker genes, which grant a selective benefit to cells that have been successfully transformed. Such markers usually confer resistance to antibiotics or herbicides and serve as essential instruments in genetic engineering (69, 70).

Transcriptomics and TEexpression

The study of cytoplasmic signaling pathways and signal-induced activation of transcription factors (TFs) has traditionally received the greatest attention within the signaling field. While genome-wide expression techniques such as RNA sequencing can detect transcripts originating from transposons, many computational pipelines tend to exclude or misinterpret TE-derived reads (10,71). Messenger RNAs (mRNAs) carry genetic information from DNA to guide protein production, a process aided by various non-coding RNAs (ncRNAs), including small nuclear RNAs (snRNAs), ribosomal RNAs (rRNAs), and transfer RNAs (tRNAs) (72). Recent technological improvements have enhanced the ability to pinpoint expressed TE loci and to distinguish between transcripts that drive TE mobilization and chimeric gene–TE transcripts, where transposable elements are co-transcribed alongside genes (10) in which TEs are co-transcribed with genes, and pervasive transcription that generates diverse RNA species distinct from protein-coding RNAs and canonical ncRNAs such as tRNAs, rRNAs, snRNAs, and snoRNAs (73).

The formation of transposable element (TE)-derived non-coding RNAs in plants, including both small non-coding RNAs (sncRNAs) and long non-coding RNAs (lncRNAs), has emerged as a major area of investigation. Among sncRNAs, heterochromatic and epigenetically active siRNAs are generated from TEs and play significant roles in shaping gene regulation and epigenetic patterns (74). These RNA molecules are essential for suppressing transposable elements, ensuring genome integrity, and influencing the control of gene expression. In microorganisms, TE-derived small RNAs and lncRNAs regulate transposition, stress responses, and pathogenic traits (74, 75). The principal challenges associated with detecting TE expression include issues of mappability, insertional polymorphisms, and internal sequence variation, all of which complicate accurate annotation and quantification.

Conclusion

Transposons constitute versatile genetic tools with wide-ranging applications in fungal genomics, mutagenesis, and biotechnology. Their classification, mobility, and interactions with host defense systems profoundly influence genome architecture and evolutionary trajectories. Ongoing advances in bioinformatics and transcriptomics are steadily improving the understanding of transposable element dynamics, thereby opening new avenues for strain improvement, functional genomics, and molecular diagnostics.

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