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Popular Article

The influence of transposable elements on plant pathogen evolution

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Introduction

Transposable elements (TEs) are the DNA sequences that have ability to change their position within a genome. These are also called as jumping genes, junk DNA, selfish DNA *etc*. TEs are present in every prokaryotic and eukaryotic genome and make up a large fraction of the genome and are responsible for much of the mass of DNA in a eukaryotic cell. Although TEs are selfish genetic elements, many are important in genome function and evolution. Transposons are also very useful to researchers as a means to alter DNA inside a living organism. As a result of their deep evolutionary origins and continuous diversification, TEs come in a bewildering variety of forms and shapes. Transposition often results in duplication of the same genetic material. Transposable elements were discovered by Barbara McClintock in 1965 through an analysis of genetic instability in maize and earned a Nobel Prize in 1983.

Characteristics of transposable elements

i. They code for enzymes which result in self-duplication and insertion into a new DNA site
ii. Because transposons carry the genes for initiation of RNA synthesis, some previously dormant genes might be activated
iii. It doesn't have a site for the origin of replication. As a result, it cannot replicate without the host chromosome as plasmids or phages
iv. There is no homology between the transposon and its target site for insertion
v. These elements can insert at almost any position in the host chromosome or a plasmid

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vi. Some transposons might seem likely to enter at some specific positions (hot spots), they barely insert at base-specific target sites

Classification of transposable elements

TEs can be divided into two major classes based on their mechanism of transposition and each class can be subdivided into subclasses based on the mechanism of chromosomal integration (Table 1). Class 1 elements, also known as retrotransposons, mobilize through a 'copy-and-paste' mechanism whereby a RNA intermediate is reverse-transcribed into a cDNA copy that is integrated elsewhere in the genome (Boeke *et al*., 1985). For long terminal repeat (LTR) retrotransposons, integration occurs by means of a cleavage and strand-transfer reaction catalyzed by an integrase much like retroviruses (Brown *et al*., 1987). For non-LTR retrotransposons, which include both long and short interspersed nuclear elements (LINEs and SINEs), chromosomal integration is coupled to the reverse transcription through a process referred to as target-primed reverse transcription (Luan *et al*., 1993). Class 2 elements, also known as DNA transposons, are mobilized *via* DNA intermediate, either directly through a 'cut-and-paste' mechanism or in the case of Helitrons, a 'peel-and-paste' replicative mechanism involving a circular DNA intermediate.

Table 1: The hierarchical classification of transposable elements

Level	Description
Class	It divides transposable elements (TEs) into two classes based on their transposition intermediate: RNA (class I or retrotransposons) or DNA (class II or DNA transposons).
Subclass	It separates TEs that transpose via "copy-and-paste" mechanism from those *via* "cut-and-paste" mechanism.
Order	It distinguishes TEs with different insertion mechanisms due to dissimilar encoded enzymes
Superfamily	Superfamilies within an order share the same insertion mechanism but are different in terms of enzyme organization, non-coding domains and/or TSD
Family	It is defined by DNA sequence conservation.
Subfamily	It is defined on the basis of phylogenetic data and might serve to differentiate autonomous and non-autonomous derivatives.

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Each TE subclass is further divided into subgroups (or superfamilies) that are typically found across a wide range of organisms, but share a common genetic organization and a monophyletic origin. For example, Ty3/*gypsy* and Ty1/*copia* elements are the two major superfamilies of LTR retrotransposons that occur in virtually all major groups of eukaryotes (Malik and Eickbush, 2001). Similarly, Tc1/*mariner*, *hAT* (hobo-Ac-Tam3) and MULEs (Mutator-like elements) are three superfamilies of DNA transposons that are widespread across the eukaryotic tree (Feschotte and Pritham, 2007). At the most detailed level of TE classification, elements are grouped into families or subfamilies, which can be defined as a closely related group of elements that can be traced as descendants of a single ancestral unit. This ancestral copy can be inferred as a consensus sequence, which is representative of the entire (sub) family (Britten and Kohne, 1968). Thus, in principle, every TE sequence in a genome can be affiliated to a (sub) family, superfamily, subclass and class (Fig. 1). However, much like the taxonomy of species, the classification of TEs is in constant flux, perpetually subject to revision due to the discovery of completely novel TE types, the introduction of new levels of granularity in the classification, and ongoing development of methods and criteria to detect and classify TEs.

Transposons further can be classified as either "autonomous" or "non-autonomous" in both Class I and Class II TEs. Autonomous TEs can move by themselves, whereas non-autonomous TEs require the presence of another TE to move. This is often because dependent TEs lack transposase (for Class II) or reverse transcriptase (for Class I).

Functions of transposable elements

TEs: Adaptive drivers of evolution

Genome plasticity enables organisms to adapt to environmental changes and occupy novel niches. Adaptive evolution mediated by TEs is facilitated by recombination events resulting in genomic diversification. This is achieved through genomic changes, which persist under positive selection in fungal pathogens. TEs contribute towards adaptive genetic variation through:

(1) TE insertion into coding genes (Jangam *et al*., 2017)
(2) TE insertion into introns
(3) TE transposition in proximity to genes
(4) Generation of retro copies *via* reverse transcription and
(5) Aberrant transposition and ectopic recombination through paralogous TEs.

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TEs: Structural transformers of the genome

Genome plasticity can be described as alterations observed in a genome structure, which can be characterized by changes in genome organization, chromosome number and genome size. Genome plasticity is mainly influenced by environmental stresses faced by individual genes in host species that confer genetic adaptability traits for survivability where TEs may play an assistive role (Belyayev, 2014). Eukaryotic genome plasticity can be caused by TE-mediated chromosomal rearrangements through ectopic homologous recombination or alternative transposition. Furthermore, the mutation caused by TE insertion may also lead to generation of new proteins promoted by exon shuffling and TE domestication (Castanera *et al*., 2016). TE insertions within functional genes may bring about alternative splicing resulting in altered protein synthesis. All of these TE insertion-promoted processes, *viz*., exon shuffling, TE domestication and exonization, can generate novel genes with possible specific functions in the host (Fig. 1).

TEs: Mediators of pathogenicity and host range

Effector proteins that are secreted by fungal pathogens to promote colonization interfere with host defense and result in necrosis. By the same token, effector proteins can be recognized by their complementary plant resistance genes, leading to the activation of defense responses in plants (Venner *et al*., 2009). Pathogenicity genes that are often clustered within a specific region of the genome codes for these molecules that promote infection of host plants. TEs' recurring association with pathogenicity can be seen by looking at the positional aspect. TEs often sit in proximity with pathogenicity factors as seen in *M. oryzae* where genes that encode secreted proteins are found within 1 kb flanking distance from TEs (Bao *et al*., 2017).

TE insertion mediates pathogenicity through mutational effects on pathogenicity-associated genes. Mutations from TE insertions can lead to genetic variability that generates many new pathogenic variants with conferred ability to invade previously resistant host plants (overcome host plant resistance) and thence expand on its host range. TE mediated inactivation or deletion of PAMP-encoding genes or effector genes important for host recognition results in gain of virulence (Fig. 1) by evading the plant's immune system (Dean *et al*., 2005). A genomic region occupying *Avr4/6* in *Phytophthora sojae*, which is responsible for virulence in soybean, revealed a Ty1/*Copia*-like

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element in proximity to this locus. This TE insertion caused point mutations conferring virulence to this locus (Basnayake *et al*., 2009).

Transposable elements in plant pathogenic fungi

In fungi they were first identified in the yeast *Saccharomyces cerevisiae* (Boeke, 1989) but only very recently in filamentous fungi. Despite extensive investigation of molecular genetics of some species used as models for fungal genetics, exemplified by the well-studied ascomycetes *Neurospora crassa* and *Aspergillus nidulans*, no evidence for the activity of transposable elements has been revealed that might be the consequence of continuous selection for phenotypic stability.

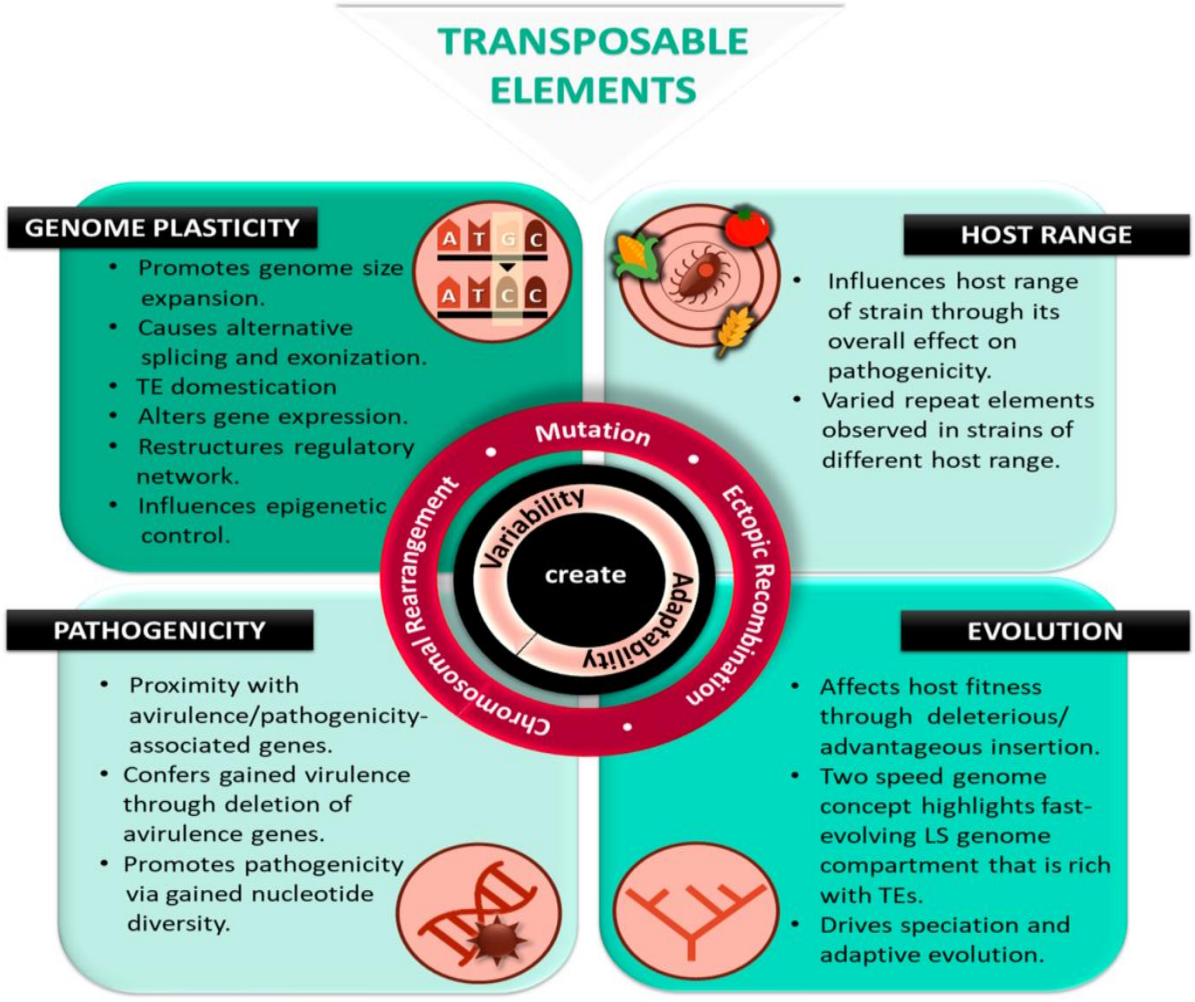

Fig. 1. The role of transposable elements in affecting genome plasticity, influencing host range and pathogenicity and shaping evolution of phytopathogens

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Paradoxically, most of our knowledge of TEs in fungi comes from studies on undomesticated species: plant pathogens, industrial and field strains. Most of these species lack the sexual stage and generally exhibit a high level of genetic variation, which attracts speculation that they contain active transposons.

Fungal TEs have been identified by a variety of strategies, mainly by the characterization of dispersed repetitive sequence or by trapping them in a target gene. The nitrate reductase gene has been particularly useful for this purpose because chlorate resistance can select loss-of-function mutants (Daboussi, 1997). Other elements were found by heterologous hybridization or polymerase chain reaction (PCR) amplification with degenerated primers deduced from conserved domains (Daboussi, 1997). Finally, as genome segments began to be cloned and sequenced, the discovery of new TEs accelerated (Cambareri *et al*., 1998). The TEs presented in Fig. 3 are found in three orders of fungi, Ascomycota, Basidiomycota and Zygomycota. However, most were identified in Ascomycota species. This bias is probably due to the number of researchers working on ascomycetes, using *A. nidulans, N. crassa, A. immersus* and *Podospora anserina* as models, or their involvement in plant interactions and biotechnology processes. The 60 TE sequences have been assigned to the major groups previously described in the different kingdoms (Capy *et al*., 1997).

Transposable elements in plant pathogenic bacteria

There are two main types of transposable elements in bacteria having different size and structure.

1. Insertion sequences (IS elements)
2. Prokaryotic Transposons (Tn): Composite and non-composite transposons

Insertion sequences:

These are simplest type of bacterial transposable sequences that can insert at different location of bacterial chromosome and plasmid through illegitimate recombination. They are typically short sequences and contain only one gene that encodes the enzyme for transposition. A bacterial chromosome may contain several copies of a particular type of IS element

Characteristics of Insertion sequences

1. IS elements are compactly organized and containing about 1000 nucleotide pairs and contain only genes (open reading frame) which encode for enzyme for regulating transposition.

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2. Many distinct types of IS elements have been identified. The smallest IS element is IS*1* which is 768 nucleotide pairs long.
3. Each type of IS element contains inverted terminal repeats at both end and a transposon sequence in between those inverted repeats. Transposon is the only gene that code for transposition of IS element.
4. The inverted terminal repeats is 9-40 base pair long and is the characteristics of most IS element
5. IS element have the capacity to duplicate the inserted sequence at the site of insertion; known as target site duplication.

Transposition of insertion sequence in bacteria

IS element containing single open reading frame (ORF) which encodes for the enzyme transposase, catalyzing its own transposition. The enzyme transposase is like restriction endonuclease which binds to terminal inverted repeats (IR) of IS element which is the restriction site. Then the enzyme cut and excise IS elements from chromosome or plasmid. The excised IS element is mobile in nature and moves along the length of chromosome to recognize the target site for insertion on same or different chromosome or plasmid. Once recognizing the target site, it generates staggered cleavage (cut the single strand of DNA) generating sticky and itself gets inserted. As IS element get inserted, the proofreading mechanism of DNA results in duplication of the DNA sequence at the target site of the insertion such that one copy of target DNA is located on each side of IS element. Thus, IS elements helps in target site duplication.

Prokaryotic Transposons (Tn)

Prokaryotic Transposons are similar to IS element but they are larger and also contain other genes (mostly antibiotic resistance gene) in addition to gene that encode transposase. Transposons are several thousand base pairs long and contain inverted terminal repeats. There are two types of prokaryotic transposons- composite and non-composite transposons. The composite transposons and Tn3-like elements are more complex than IS elements, containing some genes that encode products unrelated to the transposition process.

Composite transposons: Composite transposons are created when two IS elements insert near each other and the region between the two IS elements can then be transposed when the elements act jointly. For example, Tn10 is composite transposons of 9.3kbp which contains 1.4 kbp terminal

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inverted repeats and in between them is gene for transposase and gene for antibiotic resistance (Fig. 2).

Non-composite transposons: The non-composite transposons are a sequence of DNA containing gene for trasnposase and multiple other genes in between terminal inverted repeats. Unlike composite transposons, it does not contain IS elements at each end but instead it contains simple inverted repeats of 38-40 nucleotide pairs at each end. For example, Tn3 is non-composite transposons of 5kbp which contains three gene for beta-lactamase (bla), transposase (tnpA) and resolvase (tnpB). The beta lactamase provide resistance to the antibiotic ampicillin, and the other two enzymes play important roles in transposition and recombination (Fig. 3).

ISs can generate significant variability in bacteria and contribute to their evolution (Jackson *et al*., 2011) in part because they are usually present in more than one copy per genome and thus represent mobile regions of recombination. Their mobility, together with their capacity to mobilize unrelated DNA in their proximity, can lead to panoply of mutations and rearrangements in the host bacteria, which include insertions, deletions, duplications, translocations, co integrations, inversions and gene activation (Craig *et al*., 2002). From these activities, it easily follows that they have an enormous potential to alter the genome and influence bacterial evolution. They can also shuffle DNA among different genetic replicons such as chromosomes and plasmids sustaining a gene trading activity that widely contributes to the horizontal spread of genetic information.

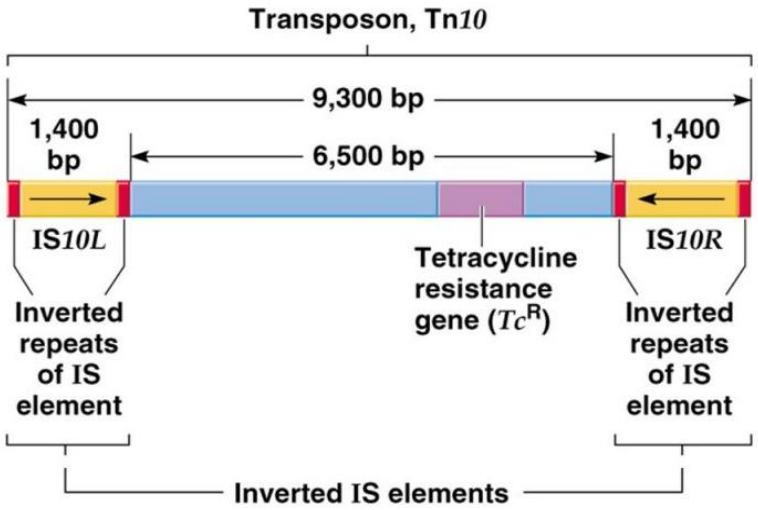

Fig 2. Composite transposons in bacteria

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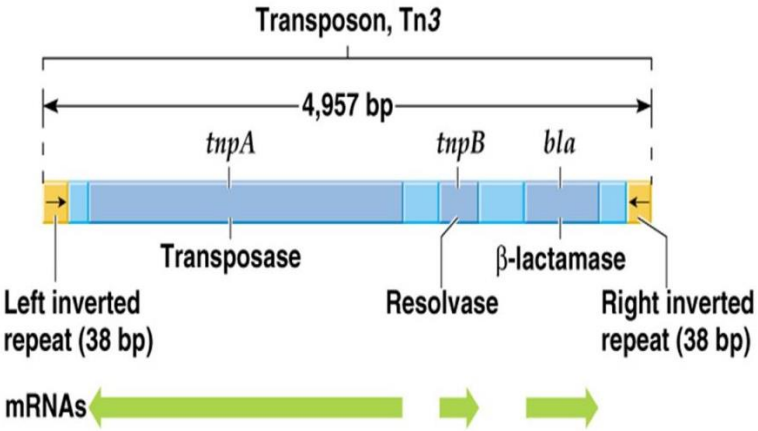

Fig. 3. Non-composite transposons in bacteria

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