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Using rice to understand the origin and amplification of miniature inverted repeat transposable elements (MITEs)

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Recent studies of rice miniature inverted repeat transposable elements (MITEs), largely fueled by the availability of genomic sequence, have provided answers to many of the outstanding questions regarding the existence of active MITEs, their source of transposases (TPases) and their chromosomal distribution. Although many questions remain about MITE origins and mode of amplification, data accumulated over the past two years have led to the formulation of testable models.

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Abbreviations

IS*5*	insertion sequence *5*
MITE	miniature inverted repeat transposable element
MLE	*Mariner*-like element
ORF	open reading frame
PIF	*P instability factor*
Tc1	transposon of *Caenorhabditis elegans* 1
TE	transposable element
TIR	terminal inverted repeat
TPase	transposase
TSD	target site duplication

Introduction

The transposable elements (TEs) discovered in maize by Barbara McClintock [1] are now called class 2 or DNA transposons. This is to distinguish them from class 1 transposons or retrotransposons, which are not the subject of this review. DNA transposons usually have short terminal inverted repeats (TIRs) and encode a transposase (TPase). This TPase binds in a sequence-specific manner to the ends of the TPase-encoding element and to other non-autonomous elements that do not encode TPase but have the same or very similar TIRs. TPases are a group of diverse enzymes that have been used to classify DNA transposons into superfamilies that are mobilized by related TPases. For example, the maize *Ac* element is a member of the *hAT* superfamily, which includes elements such as *hobo* from *Drosophila* and *Tam3* from *Antirrhinum* that have related TPases.

Miniature inverted repeat transposable elements (MITEs) are a subset of non-autonomous DNA transposons that have a suite of characteristics that distinguish them from other class 2 non-autonomous elements. MITE families have very high copy number (up to several thousand copies), structural homogeneity, and phylogenies that are consistent with rapid and extensive amplification of one or a few 'master' copies followed by inactivity and drift [2-4,5•]. Because MITEs do not encode any TPase or TPase remnant, their classification has been based on shared TIR and target site duplication (TSD) sequences. In plants, most MITEs fall into one of two superfamilies; they are either *Tourist*-like or *Stowaway*-like on the basis of their similarity to two elements originally identified in maize and sorghum, respectively [4,6,7]. Both groups are distinguished from all previously described plant transposons by their having a target sequence preference (i.e. TAA for *Tourist*-like and TA for *Stowaway*-like MITEs). Whereas DNA transposons were originally isolated from unstable mutant alleles, virtually all MITEs have been identified through computer-assisted database searches. In this way, *Tourist*-like MITEs have been shown to be widespread in plants and animals, whereas *Stowaway*-like MITEs are widespread in plants [3].

A survey of mined plant MITEs from the rapidly expanding database indicates that there are MITE families that may not fit into either of the major groups [8–11]. Some of these families are likely to be derived from established plant DNA-transposon superfamilies such as CACTA, *hAT* or *Mutator* [3,11,12]. In a few cases, the copy number of these elements was reported to be in the thousands [13], but these MITE families are not discussed in this review because they are poorly represented in *Arabidopsis* and rice.

MITEs: the highest-copy-number TEs in rice

Although MITEs were first discovered in maize, the paucity of maize genomic sequence has restricted the questions that could be answered in this member of the grass family. The value of rice genomic sequence in MITE research was apparent from the first systematic study of the repetitive DNA in 105 rice genes, all of the available rice genomic sequence at the time. The results of this study demonstrated that there are many families of MITEs in rice, and that MITEs were the most abundant TE type in the non-coding regions of rice genes [14].

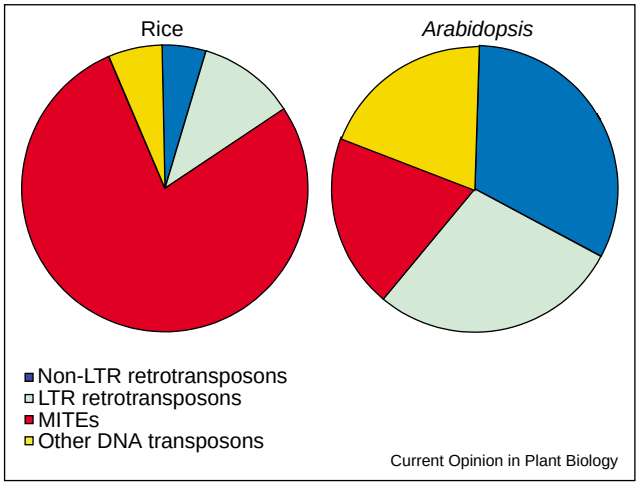
Since the initiation of the International Rice Genome Sequencing Project (IRGS) in 1998 [15], the availability of increasing quantities of genome sequence has enabled

comprehensive analyses of MITEs and other rice TEs. Rice has been validated as a model grass for the study of DNA transposons as it has become apparent that its genome contains virtually all the major element families found in other grasses [9,16,17]. In addition, the wealth of rice resources, including the genomic sequences of the two cultivated subspecies (*indica* and *japonica*) and the availability of thousands of diverse cultivars, provides the material necessary to analyze the impact of TEs on genome evolution [18,19].

A key challenge to the genome-wide analysis of MITEs has been the identification of all MITE sequences in a given genome. Because of their lack of coding capacity and low interfamily sequence similarity [14], new MITE families cannot be easily identified on the basis of sequence similarity to known families using programs such as BLAST or RepeatMasker. Instead, several new computational tools have been developed for MITE identification. RECON is a program that recovers all classes of repetitive sequence (including MITEs, see below; [20•]). FINDMITE identifies MITEs on the basis of their structural features, such as the presence of TIRs and TSDs [21]. MITE analysis kit (MAK) is a program specifically developed to extract known MITE family members and to identify related TPase-encoding elements present in the same database [22•]. MAK has been successful in linking two rice MITE families with their respective autonomous elements [22•].

Approximately 26% of the rice genome sequence is derived from TEs; of this, the amounts derived from class 1 and class 2 elements are comparable (15% and 11%, respectively) [23]. The rice genome contrasts with the larger grass genomes in which long terminal repeat (LTR) retrotransposons account for more than half of the genomic DNA [24]. In terms of element copy number, however, the rice genome contains far more class 2 elements than class 1 elements, largely because of the presence of around 90 000 MITEs (Figure 1). Analysis of the sequences of assembled rice chromosomes revealed that MITEs are mainly distributed in the chromosomal arms (i.e. in gene-rich regions), whereas retrotransposons are concentrated in the heterochromatic regions around the centromeres [25,26]. Unlike the situation in the rice genome, the *Arabidopsis* genome contains almost equal numbers of copies of class 1 and class 2 elements (Figure 1). However, the different types of TEs in *Arabidopsis* occupy the same chromosomal niches as those in rice, with most class 1 elements being located in pericentromeric regions whereas MITEs and other class 2 elements are enriched in the gene-rich chromosomal arms [5•,27,28].

Figure 1



The relative contributions of different TE groups to the total TE copy number in rice and *Arabidopsis*. Copy numbers of rice TEs were extrapolated from Jiang and Wessler [23], Turcotte *et al.* [9], and Goff *et al.* [18]. The copy numbers of *Arabidopsis* TEs are taken from the *Arabidopsis* Genome Initiative [27] and C Feschotte (unpublished data).

Isolation of an active MITE

A major obstacle to the further characterization of MITEs was overcome when the first active MITE was isolated from rice. Three studies, published simultaneously, reported that the first active rice DNA transposon was a 430 bp *Tourist*-like MITE called *mPing*. In one study, a chromosome walk to an unstable, γ-ray-induced allele of *slender glume* (*slg*) led to the identification of *mPing* [29••]. Excision of *mPing* from the *slg* allele, which resulted in the reversion to wildtype, provided the first direct evidence that MITEs are capable of both insertion and excision. In another study, *mPing* was identified following its activation in a cell culture derived from anthers of Nipponbare rice, a *japonica* cultivar [30••]. In addition, a putative autonomous element, called *Ping*, was co-activated with *mPing*. *Ping* is a 5353 bp element and its terminal sequences (of 252 bp and 178 bp) are identical to those of *mPing* except for a single base-pair mismatch, clearly indicating that *mPing* is a recent deletion derivative of *Ping*. In the third study, *mPing* was identified through a novel computational approach that utilized RECON, a program for *de-novo* repeat identification [20•,31••]. Manual inspection of more than 1200 repeat families led to the identification of *mPing* as a candidate for an active MITE. Activity was confirmed following transposon display analysis of the DNA from an *indica* cultivar (called C5924) and its derived cell line (which had previously been shown to activate retrotransposons *Tos10*, *Tos17*, and *Tos19* [32]). Transposon display is a modified amplified fragment length polymorphism (AFLP) technique that can visualize hundreds of TE insertions simultaneously [4]. Thirty-two out of 35 new insertions of *mPing* in the cell line were into single-copy sequences of the rice genome, suggesting that the previously noted association of MITEs with genes most probably reflects a strong insertion preference.

A puzzling result from the third study was the failure to detect the putative autonomous *Ping*, either in C5924 or in any of the other *indica* cultivars tested. Thus, although *mPing* is clearly a deletion derivative of *Ping*, it has not been mobilized in the C5924 cells by using the products of *Ping*. Instead, a database search identified a related element, *Pong*, as the most likely source of TPase for *mPing*. Consistent with such a role, *Pong* was transpositionally co-activated with *mPing* in the C5924 cells [31••].

Pong and *PIF* are the likely autonomous partners of *Tourist* MITEs

Pong is related to an active transposon from maize, *P Instability Factor* (*PIF*), and both elements are founding members of the newly described superfamily of eukaryotic DNA transposons called *PIF*/IS*5* (insertion sequence *5*) [33]. Elements in this superfamily harbor two open reading frames (ORFs): ORF1 and ORF2. ORF1 may encode a DNA-binding protein, as it contains a domain with weak similarity to the *myb* DNA-binding domain [31••,34•]. ORF2 probably encodes the TPase, as it contains an apparent DDE catalytic motif and shares amino-acid homology with the TPases of some IS*5*-like bacterial insertion sequences. Members of the *PIF*/IS*5* superfamily also have similar TIRs and target-site specificity. Recently, a comprehensive survey revealed the presence of *PIF*/IS*5*-like TPases in a large number of plant, animal and fungal taxa [34•]. In plants, *PIF*/IS*5* elements comprise two clades (*PIF*-like and *Pong*-like), each represented by multiple distinct lineages that diverged before the separation of monocots and dicots [34•].

A genome-wide survey of the *PIF*/IS*5* superfamily in rice resolved more than 200 TPase-encoding elements, belonging to 27 *PIF*-like families (*OsPIFs*) and 26 *Pong*-like families (*OsPongs*) [34•]. Once these elements were identified, their relationships with *Tourist*-like MITEs could be established. Most *Tourist*-like MITEs (28 of 31 families tested; ~45 000 elements) in rice could be associated with either the *OsPIF* or the *OsPong* families on the basis of TIR sequence identity and/or additional sequence similarity in their sub-terminal regions [34•]. Approximately 60% of the *Tourist*-like MITE families, however, lacked sequence similarity beyond their TIRs with any existing *OsPIFs* or *OsPong*s. Both this result and the co-mobilization of *mPing* with *Pong* in the C5924 cell line raise the interesting possibility that many families of *Tourist*-like MITEs have been mobilized by elements from which they have not descended by deletion.

Associations between *PIF*/IS*5* elements and *Tourist*-like MITEs have also been documented in maize and *Arabidopsis* [33,35]. For example, the founding member of the superfamily, *PIF* from maize, is related to a family of *Tourist*-like MITEs called *mPIF* [33]. Although *PIF*/IS*5* elements have not been well characterized in animals, relationships of *PIF*/IS*5* elements with *Tourist*-like MITEs have been reported in nematodes, insects and fish [3,36–38]. The best examples are from the genome of the African malaria mosquito (*Anopheles gambiae*), in which at least three of the 11 *PIF*/*Pong*-like families have clearly given rise to *Tourist*-like MITEs (X Zhang, SR Wessler, J Tu, unpublished data).

Mariner-like elements are the likely autonomous partners of *Stowaway* MITEs

As mentioned above, most plant MITEs have been classified as either *Tourist*-like or *Stowaway*-like. From the initial discovery of *Stowaway* elements almost a decade ago, similarity was noted between these elements and members of the well-characterized DNA transposon superfamily Tc1/*mariner*: the two groups of elements have the same TSD (5′-TA-3′) [6]. However, Tc1/*mariner* elements were thought to be absent or rare in plants, whereas hundreds of these elements had been described in animals and fungi [39–42].

A series of studies indicate that Tc1/*mariner* transposons are actually widespread and diverse in plant genomes, and have probably given rise to very large populations of MITEs [43,44•]. Evidence connecting a plant MITE family with a Tc1/*mariner* transposon was first obtained by analyzing the genome sequence of *Arabidopsis*. Homology-based searches revealed that *Emigrant*, the first MITE family to be identified in this species with about 200 copies [45], probably originated by internal deletion from the larger *Lemi1*, which has coding capacity for a *pogo*-like TPase [43]. *Pogo*-like elements form a distinct subgroup of the Tc1/*mariner* superfamily, with representatives previously described in invertebrate, vertebrate and fungal species [41,46].

There appear to be no (or only a few) *Emigrant*-like MITEs or *pogo*-like elements in the rice genome. There are, however, tens of thousands of *Stowaway*-like MITEs in rice and in the genomes of a wide range of flowering plant taxa [6,9,14,23]. If Tc1/*mariner* elements have mobilized *Stowaway* MITEs, it follows that Tc1/*mariner* should also be widespread in the genomes of flowering plants. This was shown to be true using a combination of database searches and a polymerase chain reaction (PCR)-based approach that exploited newly designed plant-specific primers for *mariner*-like TPases [44•]. Phylogenetic analyses of more than 100 TPase sequences revealed the existence of multiple, divergent and ancient lineages of a plant-specific group of *mariner*-like elements (MLEs), which harbor a distinctive 'DD39D' signature in their TPases [44•]. These results suggest that the sequence diversity of MITEs within and among plant genomes reflects a diversity of *trans*-activating TPases, and provides support for the hypothesis that MLEs are the autonomous elements responsible for the spread of *Stowaway* MITEs in many plants.

Recently, this hypothesis was tested further by taking an inventory of the MLE and *Stowaway* families that co-exist in the rice genome and analyzing their sequence relationships in detail [47••]. The rice MLEs (called '*Osmar*' elements) were grouped into 26 families, with fewer than three full-length members per family. By contrast, more than 22 000 *Stowaway* MITEs were identified and grouped into 36 families with copy numbers ranging from a few dozen to several thousands. Comparison of all *Osmar* and *Stowaway* elements led to the surprising discovery that sequence similarity was restricted to their TIRs, and that association between the *Osmar* and *Stowaway* families was confined to characteristic motifs in their TIRs. These motifs were, in turn, diagnostic of distinct phylogenetic clades of MLE TPase. Together, these results provide evidence for a functional relationship between *Stowaway* MITEs and *Osmar* TPases [47••].

Cross-mobilization and the amplification of MITEs

Taken together, comparative analyses among the 90 000 MITEs and about 250 *PIF*-like, *Pong*-like and *mariner*-like transposons present in the rice genome uncovered surprisingly few instances of MITE families that are directly related to larger elements [34•,47••]. One way to explain this situation is to view the origin and the amplification of MITEs as two separate steps that can occur at different times. That is, MITE precursors may have originated through internal deletion of ancient (and now extinct) autonomous elements, but their amplification occurred later when transposase encoded by younger autonomous elements fortuitously recognized the older MITE and catalyzed its transposition. In this scenario, the young autonomous elements are presumably descendants or 'cousins' of the elements that gave rise to the founding MITE. According to this model, the majority of MITEs in rice have been amplified in this way by the process called cross-mobilization [47••].

An alternative explanation is that MITE amplification was followed by the loss of parental autonomous elements from the genome; that is, there has been a differential retention of MITEs rather than autonomous copies over time [47••]. MITEs, with their small size and very high copy numbers, may have a greater chance of persisting and accumulating in genomes than larger and low-copy-number elements, which might be eliminated more rapidly by drift and/or selection. The discovery that the *mPing* family was not mobilized in C5924 cell culture by the element it was derived from, *Ping*, but is most probably mobilized by *Ping*'s relative *Pong* supports the notion that cross-mobilization plays a central role in the amplification of MITEs [31••].

Conclusions

MITEs were discovered more than a decade ago as short repetitive elements that associated with many genes in grass species. Although numerous MITEs were subsequently identified and characterized in other plants as well as in animals, the origin and TPase sources of these small elements remained mysterious. The recent availability of large quantities of genomic sequence, especially from rice, has facilitated a variety of studies that have answered many questions and furnished material necessary for future analysis. It is now clear that MITEs are non-autonomous DNA elements that are capable of both insertion and excision. Their association with genes is most likely due to a strong insertion preference for low-copy sequences. The majority of MITEs have most probably originated from two large and diverse superfamilies of DNA elements, Tc1/*mariner* and *PIF*/IS5. Future studies will undoubtedly focus on the interaction of MITEs and their autonomous partners, the regulation of MITE transposition, and the impact of MITE amplification on host genomes. Clearly, rice will continue to play a central role in MITE research.

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