

Transposon-mediated epigenetic regulation contributes to phenotypic diversity and environmental adaptation in rice

Xianwei Song and Xiaofeng Cao



Transposable elements (TEs) have long been regarded as 'selfish DNA', and are generally silenced by epigenetic mechanisms. However, work in the past decade has identified positive roles for TEs in generating genomic novelty and diversity in plants. In particular, recent studies suggested that TE-induced epigenetic alterations and modification of gene expression contribute to phenotypic variation and adaptation to geography or stress. These findings have led many to regard TEs, not as junk DNA, but as sources of control elements and genomic diversity. As a staple food crop and model system for genomic research on monocot plants, rice (*Oryza sativa*) has a modest-sized genome that harbors massive numbers of DNA transposons (class II transposable elements) scattered across the genome, which may make TE regulation of genes more prevalent. In this review, we summarize recent progress in research on the functions of rice TEs in modulating gene expression and creating new genes. We also examine the contributions of TEs to phenotypic diversity and adaptation to environmental conditions.

Address

State Key Laboratory of Plant Genomics and National Center for Plant Gene Research, CAS Center for Excellence in Molecular Plant Sciences, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China

Corresponding author: Cao, Xiaofeng (xfcao@genetics.ac.cn)

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Introduction

Epigenetics refers to heritable changes in gene expression that occur without alteration of the underlying DNA sequence. Transposable elements (TEs) are major carriers of epigenetic marks and are subject to almost all epigenetic regulatory mechanisms in plants [1]. During the past decade, TE-mediated epigenetic regulation of

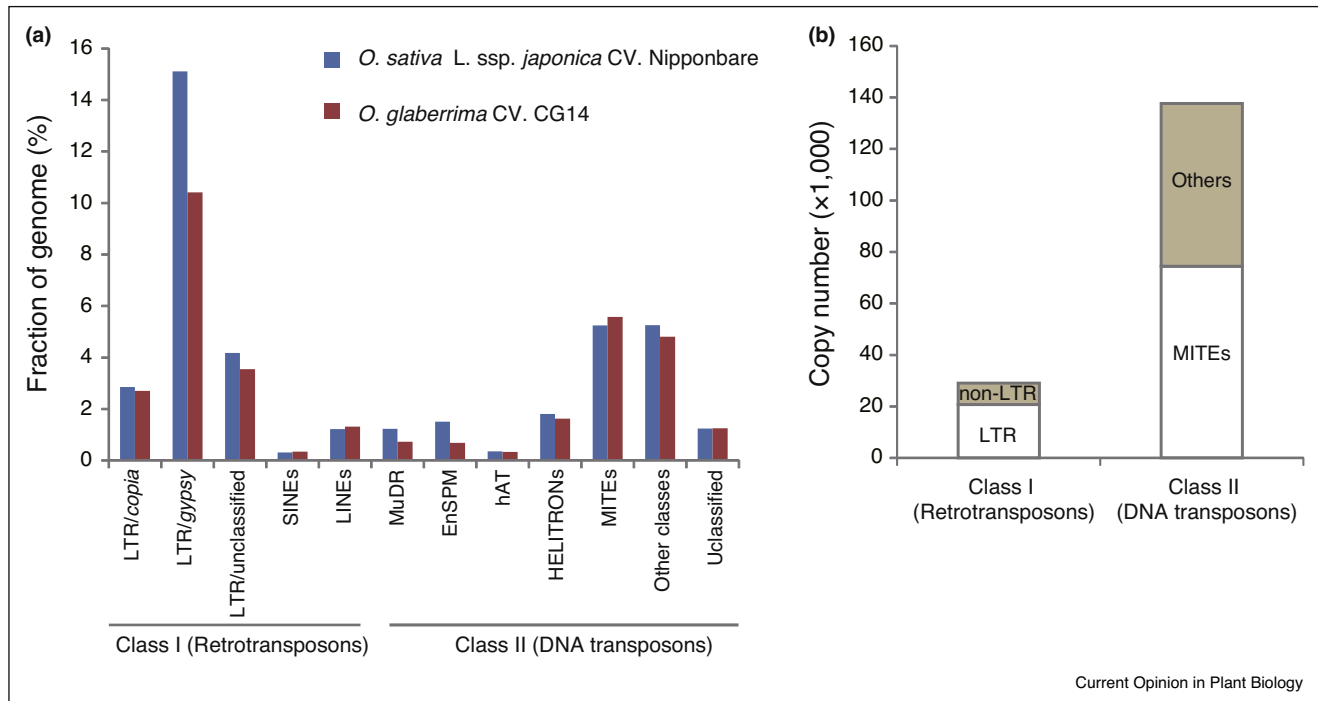
gene expression through DNA methylation, histone modification, and non-coding RNAs has gained unprecedented interest in plants. Several significant findings, such as high natural epimutation rates [2,3], identification of heritable epigenetic variants or quantitative trait loci associated with agronomic traits [4,5,6], as well as the buffering effects of epigenetic regulation under stress conditions [7], have revealed epigenetic regulation as a potential new source of beneficial traits for crop breeding.

Rice, which feeds more than half of the world's population, is a model crop for genomics studies. The rice genome contains large numbers of DNA transposons, which are scattered across the genome [8], rather than concentrated in heterochromatic regions, making it suitable for epigenetic research. Here, we briefly summarize recent advances on functional epigenetic studies, focusing on TE-mediated epigenetic regulation of rice genes.

TEs shaped the rice genome and most rice genes have associated TEs

TEs can be categorized based on their transposition mechanisms. Class I TEs (retrotransposons) transpose by a 'copy-and-paste' mechanism via an RNA intermediate; class II TEs (DNA transposons) transpose by a 'cut-and-paste' mechanism via a DNA intermediate. Both classes of TEs can be further grouped into superfamilies based on transposase specificity and sequence similarity (Figure 1a); TEs also include autonomous and nonautonomous elements, based on whether the TE encodes the proteins required for transposition. In plants, retrotransposons generally contribute to variation in genome size whereas DNA transposons preferentially insert in or near genes and contribute to the generation of allelic diversity [1]. The latter case, where DNA transposons are dispersed around the genome, may be more prominent in rice than in other plants, as rice has a moderately sized genome containing all types of plant DNA transposons (Figure 1a). Also, rice has the highest ratio (a fourfold difference in copy number) of class II to class I elements among all plant genomes that have been sequenced so far (Figure 1b) [8]. More importantly, DNA transposons display a relatively even distribution along the rice chromosomes and are significantly enriched in the 1-kb regions flanking the 5' and 3' ends of coding regions; thus, most rice genes have associated TEs [9,10,11,12,13]. In fact, analysis of the recently released

Figure 1



The diversity and abundance of TEs in rice genomes. **(a)** The diversity of different types of TEs in genomes of Nipponbare and CG14, which are representative strains of Asian and African cultivated rice, respectively. **(b)** The copy numbers of different TEs in Nipponbare. The data of (a) and (b) are from Refs. [10**] and [8], respectively. LTR: long terminal repeat; LINEs: long interspersed nuclear elements; SINES: short interspersed nuclear elements; MITEs: inverted-repeat transposable elements.

Oryza glaberrima (African cultivated rice) genome shows that more than 85% of *O. glaberrima* genes have associated TEs [10**]. Among rice genes, those associated with miniature inverted-repeat transposable elements (MITEs), the short (<600 bp), nonautonomous DNA transposons present in enormous copy numbers (Figure 1b), predominate with 23,623 (58.2%) MITE-associated genes in Asian rice (*Oryza sativa* ssp. *japonica*) and 17,796 (53.6%) in African rice (*O. glaberrima*) [10**,14].

In addition, TE-derived genes are also abundant in the rice genome. For example, the *O. sativa* genome harbors more than 10 000 copies of *Mutator*-like transposable elements (MULEs), which are DNA transposons that can capture intact or partial gene fragments and transpose them to new genomic locations, thereby potentially forming new gene structures, termed Pack-MULEs [15,16]. Genome-wide analysis identified ~2000–3000 MULE-derived putative genes in rice, which is far more than that of maize (~200–300) and *Arabidopsis* (~50) [17**,18]. Hence, TEs have shaped the rice genome and may affect the expression of many genes.

TE-based epigenetic regulation of gene expression in rice

Several mechanisms have been proposed to explain the effects of TEs on genes [1] and modulation of gene expression via epigenetic regulation has emerged as a key mechanism. This emerging understanding of epigenetic regulation of TE-associated gene has largely resulted from epigenetic research based on the high-quality genome sequences of many species produced during the past decade. Plant TEs are generally silenced by specific epigenetic mechanisms based on their sequence content and genomic locations [19–21]. Post-transcriptional silencing and transcriptional silencing of TEs, which involve interconnected regulation by small RNAs, DNA methylation, and histone modifications, are complicated, systemic processes and have been extensively described in several recent reviews [1,22–24].

Owing to extensive variation in TE content, composition, and distribution, the epigenome landscapes and epigenetic regulatory effects vary dramatically among plant species [25]. This is particularly true for rice and *Arabidopsis*, as the rice genome has more than twice

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