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Evolution of endogenous non-retroviral genes integrated into plant genomes

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ABSTRACT

Numerous comparative genome analyses have revealed the wide extent of horizontal gene transfer (HGT) in living organisms, which contributes to their evolution and genetic diversity. Viruses play important roles in HGT. Endogenous viral elements (EVEs) are defined as viral DNA sequences present within the genomes of non-viral organisms. In eukaryotic cells, the majority of EVEs are derived from RNA viruses using reverse transcription. In contrast, endogenous non-retroviral elements (ENREs) are poorly studied. However, the increasing availability of genomic data and the rapid development of bioinformatics tools have enabled the identification of several ENREs in various eukaryotic organisms. To date, a small number of ENREs integrated into plant genomes have been identified. Of the known non-retroviruses, most identified ENREs are derived from double-strand (ds) RNA viruses, followed by single-strand (ss) DNA and ssRNA viruses. At least eight virus families have been identified. Of these, viruses in the family *Partitiviridae* are dominant, followed by viruses of the families *Chrysoviridae* and *Geminiviridae*. The identified ENREs have been primarily identified in eudicots, followed by monocots. In this review, we briefly discuss the current view on non-retroviral sequences integrated into plant genomes that are associated with plant-virus evolution and their possible roles in antiviral resistance.

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1. Introduction

Viruses are infectious agents with small genome sizes that can only complete their life cycles within the living host cells of organisms of the three domains of eukaryotes, archaea, and bacteria [1]. With recent, rapid advances in the genomic analysis of viruses and hosts, it is now possible to trace the origins and evolution of viruses along with those of their hosts [1]. Horizontal gene transfer (HGT), or lateral gene transfer, is defined as the flow of genes between different species [2]. Numerous comparative genome analysis studies have revealed the wide extent of HGT in living organisms [3,4]. In particular, viruses play important roles in HGT, which contributes to the evolution and genetic diversity of living organisms.

Endogenous viral elements (EVEs) are defined as viral DNA sequences present within the genomes of non-viral organisms [5,6]. EVEs can consist of an entire viral genome or only a partial fragment.

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In eukaryotic cells, the majority of EVEs are derived from RNA viruses that use reverse transcription (RT), such as retroviruses [7,8]. In particular, plant genomes harbor a large number of endogenous plant endogenous pararetroviruses (EPRVs), as demonstrated in several recent studies [8]. EPRVs are double-stranded (ds) DNA viruses belonging to the family *Caulimoviridae* [8]. They are widely distributed in the genomes of plants, including banana, petunia, potato, rice, and tobacco [8]. A recent study revealed the genome-wide integration of endogenous banana streak virus (BSA) with 24 loci spanning 10 chromosomes; however, endogenous BSA does not appear able to form free infectious viral particles [9].

In contrast to EVEs, endogenous non-retroviral elements (ENREs) have not been well studied. However, the increasing availability of genomic data as well as the rapid development of several bioinformatics tools have enabled the identification of several ENREs in various eukaryotic organisms, including animals, insects, plants, and fungi [6,10–14]. Here, we briefly review the current view of non-retroviral sequences integrated into plant genomes associated with plant-virus evolution.

2. Approaches for identifying ENREs integrated into plant genomes

Initial efforts to identify ENREs were very difficult without any information on host genomes. The general approaches for identifying ENREs are depicted in Fig. 1. Using viral sequences as probes, cross-hybridization based approaches have been predominantly used, such as Southern blot and Western blot analyses [15,16]. For example, Southern blot analysis has been useful for estimating the copy number of a geminivirus-related DNA (GRD) in the tobacco genome [15]. With the increasing availability of genomic data for viruses and hosts, it is now possible to screen ENREs within entire genomes using BLAST tools against databases, such as the nucleotide collection (NT), genome (chromosome), reference genomic sequence (refseq_genomic), genomic survey sequence (GSS), high-throughput genomic sequence (HTGS), and whole genome shotgun (WGS) databases of the National Center for Biotechnology Information (NCBI). Indeed, most recent studies have performed intensive BLAST searches using sequences of single strand (ss) DNA and dsRNA viruses as queries [10,17–19]. It is important to generate appropriate algorithms for BLAST searches and *E*-values for thresholds. Generally, virus-like sequences have been identified at the protein level, suggesting that commonly used *E*-values for blastp, blastx, tblastn, and tblastx matches were less than 1E−5 or 1E−6. The expression of identified sequences could be verified by polymerase chain reaction (PCR) or reverse transcription (RT)-PCR followed by cloning and sequencing based on available sequences for the virus and the host. In addition, phylogenetic analysis using identified protein sequences can reveal the phylogenetic relationships of ENREs and host proteins and can provide clues regarding the evolution of ENREs along with host genes. Furthermore, the ratio of nonsynonymous (K_a) to synonymous (K_s) nucleotide substitution rates has been widely used as a measure of selective pressure on protein sequences [17]. Calculation of the K_a/K_s ratio for ENREs has provided information on their expression but also suggests that the ENREs of interest were under purifying selection. The last step in identifying ENREs might be the characterization of the functional roles of ENREs in plant genomes, which could require considerable effort and time.

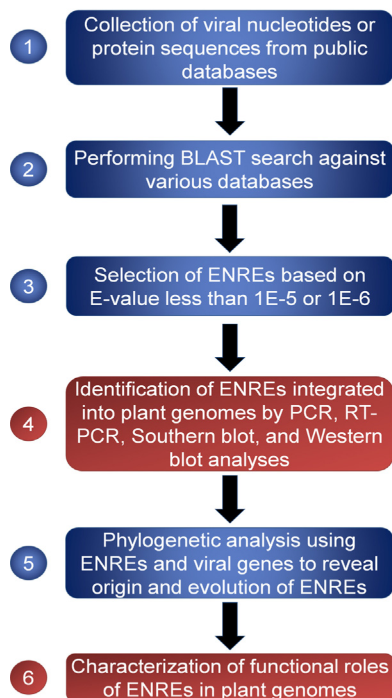

Fig. 1. Experimental approaches for identifying ENREs integrated into plant genomes. Studies identifying ENREs can be divided into two types: dry (blue box), which use various bioinformatics tools, and wet, which use laboratory experiments (red box).

3. Integration of ENREs into plant genomes

3.1. Overview of identified ENREs

To date, a small number of ENREs integrated into plant genomes have been identified. Here, we summarize these previous results (Fig. 2 and Supplementary Table 1) before describing them in detail. Of the known non-retroviruses, most identified ENREs are derived from dsRNA viruses, followed by ssDNA and ssRNA viruses (Fig. 2A). At least eight virus families have been identified. Of these, viruses in the family *Partitiviridae* are dominant, followed by those of the families *Chrysoviridae* and *Geminiviridae* (Fig. 2B). Viruses of at least 11 genera were identified that are integrated into plant genomes. Of these, unclassified viruses and partitiviruses are dominant (Fig. 2C). Identified ENREs have primarily been found in eudicots, followed by monocots. Even plants belonging to the classes Pinopsida and Prasinophyceae harbor ENREs (Fig. 2D). ENREs have been frequently identified in plants belonging to the orders Poales, Brassicales and Fabales (Fig. 2E). Some ENREs have been found to display high similarity with viral sequences. For example, 10 ENREs have been identified with an *E*-value of 0 (Fig. 2F).

Supplementary material related to this article can be found, in the online version, at doi:10.1016/j.cpb.2014.07.002.

3.2. Integration of sequences derived from dsRNA viruses in plant genomes

Among the various types of viruses, double-stranded (ds) RNA viruses have been frequently reported as giving rise to ENREs [10,17]. Interestingly, most dsRNA viruses homologous to plant genes are mycoviruses, which infect various fungi. For instance, the capsid protein (CP) of *Sclerotinia sclerotiorum* partitivirus S (SsPV-S) is homologous to the *Arabidopsis* protein IAA-leucine-resistant protein 2 (ILR2) [17]. Additionally, both the CPs of SsPV-S and ILR2 show high levels of similarity with a GEM protein of the meadow fescue (*Festuca pratensis*).

Using the protein sequences of available partitiviruses and totiviruses, a total of 22 partitivirus-like and 34 totivirus-like sequences have been found in various eukaryotic organisms, including plants [17]. Partitivirus-related ENREs have been found

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