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Endornaviruses: persistent dsRNA viruses with symbiotic properties in diverse eukaryotes

Toshiyuki Fukuhara[1]

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Abstract
Endornaviruses are unique, persistent, double-stranded RNA (dsRNA) viruses with symbiotic properties that infect diverse eukaryotes, such as plants, fungi, and oomycetes. Endornaviruses contain a linear dsRNA genome of approximately 10 to 17 kbp in length and are classified in the family *Endornaviridae*, which consists of two genera, *Alphaendornavirus* and *Betaendornavirus*. The endornaviruses encode a single long open reading frame encoding approximately 3200 to 5800 amino acid residues of conserved viral RNA helicase and RNA-dependent RNA polymerase domains, and some endornaviruses contain a site-specific nick in the coding strand of their dsRNA genome. Acute plant viruses propagate rapidly and systemically, eventually killing the host plant, and are then transmitted horizontally. In contrast, plant endornaviruses have several common persistent (symbiotic) properties: a stable low copy number in the host plant, no obvious effect on the host plant, and efficient vertical transmission via gametes. Plant endornaviruses are likely maintained within host plants for hundreds of generations, so the host must stringently regulate their propagation. Whereas RNA silencing functions as a defense system against acute viruses in plants, it may be necessary for the persistent infection (symbiotic life cycle) of endornaviruses. This process includes the stringent regulation of low virus copy number (steady replication before every host cell division) and efficient vertical transmission of the virus to the next generation.

Keywords Asymptomatic infection · DsRNA virus · Endornavirus · *Oryza sativa endornavirus* · Persistent virus · RNA silencing

Introduction

Viruses are thought to affect the phenotype of their host plant, and plants infected with viruses are thought to exhibit visible disease symptoms, such as stunting (dwarfing), yellowing, and mosaicism. Thus, infection of crop plants and vegetables with viruses severely damages their yield and quality. Consequently, extensive phytopathologic studies aimed at protecting crop plants from virus infections have been conducted, and many acute plant viruses, such as *Tobacco mosaic virus* (TMV) and *Cucumber mosaic virus* (CMV), have been studied in detail.

Commercially available crops, vegetables, and fruits are believed to be virus free. However, these products are often infected with persistent viruses [1–3], and double-stranded RNAs (dsRNAs) of viral genomes have been frequently detected in commercially available radishes [4], bell pepper fruits [5], and rice grains [6]. These dsRNAs represent the genomes of persistent viruses such as *Raphanus sativus cryptic virus 1*, classified in the family *Partitiviridae* [7], and *Bell pepper endornavirus* (BPEV) and *Oryza sativa endornavirus* (OsEV), which are classified in the family *Endornaviridae* [8]. As these crops are infected with persistent dsRNA viruses and exhibit no symptoms (i.e., they are healthy), they are safe for human consumption and thus sold commercially as food crops.

This review focuses on one of these persistent dsRNA viruses, the endornaviruses, and describes their wide distribution, molecular structures, and unique symbiotic properties that differ from those of conventional plant viruses.

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✉ Toshiyuki Fukuhara
fuku@cc.tuat.ac.jp

[1] Department of Applied Biological Sciences, Institute of Global Innovation Research, Tokyo University of Agriculture and Technology, 3-5-8 Saiwaicho, Fuchu, Tokyo 183-8509, Japan

OsEV is the most studied endornavirus, and as it is found in many cultivars of cultivated rice (*Oryza sativa* L.), it is recognized as an alphaendornavirus type species. The molecular structure, efficient vertical transmission, and copy number regulation of OsEV will be described. Furthermore, the symbiotic life cycle of endornaviruses (persistent dsRNA viruses) will be compared with the propagation strategy of acute single-stranded RNA (ssRNA) viruses that often affect the growth and development of host plants and thus cause disease symptoms. The latter have been extensively studied.

Enigmatic large dsRNAs were recognized as novel persistent viruses in the new genus *Endornavirus* within the new family *Endornaviridae*

In the 1980s, large linear dsRNAs of approximately 14 kbp in length were frequently found in rice, barley (*Hordeum vulgare*), common bean (*Phaseolus vulgaris*), and bell pepper (*Capsicum annuum*) [1–6, 8–10]. These dsRNAs had several unique common properties: (1) they were not transcribed from the host genomic DNAs; (2) they had no obvious effect on the phenotype of the host plants; (3) they were distributed throughout all tissues of the host plants at a stable low concentration; (4) they were transmitted to the next generation only through the gametes; (5) their horizontal transfer to other plants had never been proven; and (6) no obvious virus-like particles were found with these dsRNAs. Therefore, they were previously referred to as RNA plasmids [3] or enigmatic dsRNAs [6, 11].

At the turn of this century, dsRNAs from broad bean (*Vicia faba*), cultivated rice (*O. sativa*), and wild rice (*O. rufipogon*) were completely sequenced [12–14]. These dsRNAs encoded a single, long open reading frame (ORF) of approximately 4600 amino acid (aa) residues that composed the conserved viral RNA-dependent RNA polymerase (RdRp) and RNA helicase (Hel) domains (Fig. 1). Phylogenetic analyses of the two conserved domains indicated that the large dsRNA viruses share a common ancestor with the alpha-like supergroup of positive-sense ssRNA viruses, which includes many plant viruses, such as TMV and CMV [15]. Based on these data, the International Committee on Taxonomy of Viruses (ICTV) classified the large dsRNA viruses as members of a new genus, *Endornavirus*, within a new virus family, *Endornaviridae* [8, 16]. The eighth and ninth reports of the ICTV classified the family *Endornaviridae* within the dsRNA virus group [8, 16]. However, an alternative opinion based on phylogenetic analyses holds that the family *Endornaviridae* should be classified in the positive-sense ssRNA virus group, and large dsRNAs are considered their replication intermediates [17, 18].

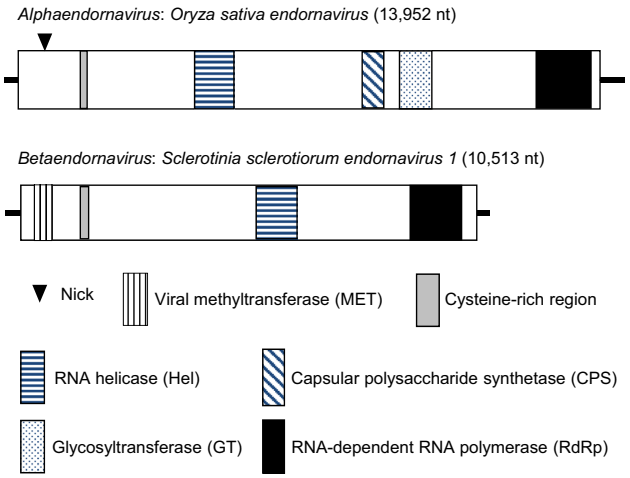

Fig. 1 Organization of the *Oryza sativa endornavirus* (OsEV) genome, the type species of *Alphaendornavirus*, and the *Sclerotinia sclerotiorum endornavirus 1* (SsEV1) genome, the type species of *Betaendornavirus*. The site-specific nick is only present in the coding strand of alphaendornaviruses

An increasing number of recent reports have described the isolation of nucleotide sequences that likely belong to viruses of the family *Endornaviridae* from plants as well as fungi and oomycetes. Currently, this family consists of two genera, *Alphaendornavirus* and *Betaendornavirus*, which are classified based on genome size and the presence of unique protein domains. To date, the genus *Alphaendornavirus* includes 19 viruses that infect plants, fungi, and oomycetes, whereas the genus *Betaendornavirus* includes 5 viruses that infect ascomycete fungi (Table 1; Fig. 2) [19].

Plant endornaviruses

A cytoplasmic male sterility (CMS) trait in the "447" strain of broad bean and cytoplasmic spherical bodies (CSBs) found in the cytoplasm of 447 plants was described just over 4 decades ago [20]. These CSBs contained a large dsRNA of approximately 17.6 kbp in length, and a correlation between the CMS trait and the presence of a CSB with a large dsRNA in the "447" strain was reported [21, 22]. The nucleotide sequence of the large dsRNA and phylogenetic analysis of its single large ORF revealed that this dsRNA is a member of the family *Endornaviridae*, and it was subsequently named *Vicia faba endornavirus* (VfEV) [12]. VfEV is the only plant endornavirus that affects the visible phenotype of the host.

Large dsRNAs of approximately 14 kbp in length were reported almost three decades ago in many cultivars of cultivated rice and one strain (W-1714) of wild rice (*O. rufipogon*), but they were not found in the *indica* subspecies of cultivated rice [6, 23, 24]. Completely sequencing of two

Table 1 Endornaviruses recognized by the ICTV

Host	Host	Name	Ab	Refs
Alpha				
Plant	Malabar spinach	*Basella alba endornavirus 1*	BaEV1	[73]
	Bell pepper	*Bell pepper endornavirus*	BPEV	[31]
	Melon	*Cucumis melo endornavirus*	CmEV	[34]
	Barley	*Hordeum vulgare endornavirus*	HvEV	[27]
	Hot pepper	*Hot pepper endornavirus*	HPEV	[32]
	Bottle gourde	*Lagenaria siceraria endornavirus*	LsEV	[36]
	Wild rice (W1714)	*Oryza rufipogon endornavirus*	OrEV	[13]
	Cultivated Rice	*Oryza sativa endornavirus**	OsEV	[14]
	Avocado	*Persea americana endornavirus 1*	PaEV1	[37]
	Common bean	*Phaseolus vulgaris endornavirus 1*	PvEV1	[29]
	Common bean	*Phaseolus vulgaris endornavirus 2*	PvEV2	[29]
	Broad bean (447)	*Vicia faba endornavirus*	VfEV	[21]
	Winged bean	*Winged bean endornavirus*	WBEV1	[74]
	Mate	*Yerba mate endornavirus*	YmEV	[75]
Fungus	Powdery mildew fungus	*Erysiphe cichoracearum endornavirus*	EcEV	[76]
	Endophyte	*Grapevine endophyte endornavirus*	GEEV	[77]
	White root rot fungus	*Helicobasidium mompa endornavirus 1*	HmEV1	[42]
	Rhizoctonia	*Rhizoctonia cerealis endornavirus 1*	RcEV1	[78]
Protista	Phytophthora	*Phytophthora endornavirus 1*	PEV1	[43]
Beta				
Fungus	Alternaria	*Alternaria brassicola endornavirus 1*	AbEV1	[79]
	Gray mold fungus	*Botrytis cinerea endornavirus 1*	BcEV1	[80]
	Gremmeniella	*Gremmeniella abietina endornavirus 1*	GaEV1	[81]
	White mold fungus	*Sclerotinia sclerotiorum endornavirus 1**	SsEV1	[19]
	Truffle	*Tuber aestivum endornavirus*	TaEV	[82]

Ab abbreviation, *Ref* reference

*The type species of *Alphaendornavirus* and *Betaendornavirus*

dsRNAs from the Nipponbare cultivar of cultivated rice and the W-1714 strain of wild rice indicated that the viruses were members of the family *Endornaviridae*, and they were thus named OsEV and *Oryza rufipogon endornavirus* (OrEV), respectively [16].

In Nipponbare, the model cultivar of cultivated rice, molecular biological analyses identified OsEV-carrying and OsEV-free plants. However, these two isogenic lines did not exhibit distinguishable phenotypes [25], and even rice breeders and farmers were unable to distinguish them. If the OsEV-carrying line had a lower harvest yield than the OsEV-free line, breeders and/or farmers would recognize this phenotype and discard the lower-yielding line.

To date, 14 endornaviruses have been found in plants, including barley [26, 27], common bean (*P. vulgaris*) [28, 29], bell and hot peppers (*C. annuum*) [30–32], melon (*Cucumis melo*) [33, 34], bottle gourd (*Lagenaria siceraria*) [35–37], and avocado (*Persea americana*) [38], and all of these viruses were classified into the genus *Alphaendornavirus* (Table 1; Fig. 2). Common cultivars of endornavirus-harboring crop plants and vegetables are now commercially available, which indicates that these plants are healthy. Current data indicate that most endornaviruses found in plants, with the exception off VfEV, cause asymptomatic and persistent infections in the host plant.

Recently, however, variations in physiologic traits have been reported in lines of common bean infected with or free of endornaviruses (PvEV1 and PvEV2), with the infected lines exhibiting significantly more rapid seed germination, longer radicles, lower chlorophyll content, higher carotene content, longer pods, and higher seed weight than endornavirus-free lines [39].

Fungal endornaviruses

A wide variety of viruses have been found in many fungi, including mushrooms and plant pathogenic fungi [40–42]. Fungal viruses are termed mycoviruses, and most contain dsRNAs as the genome. dsRNA mycoviruses are primarily classified into four families, the *Partitiviridae, Totiviridae, Chrysoviridae*, and *Endornaviridae*, but it has been

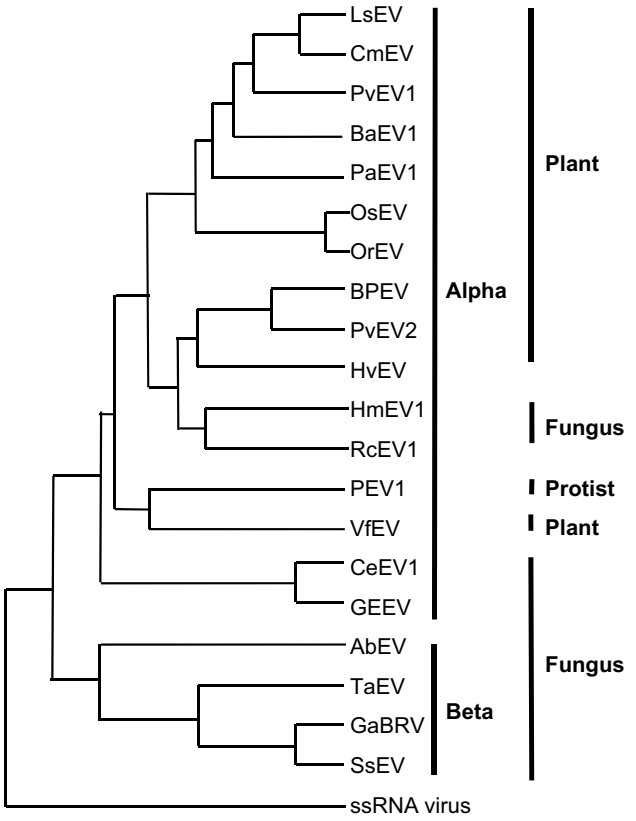

Fig. 2 Phylogenetic tree of selected endornaviruses, as modified from a tree constructed by Peng et al. [37] using the aa sequences of RdRp domains of endornaviruses. Abbreviations of virus names are indicated in Table 1

proposed that recently discovered novel mycoviruses should be classified into a new genus and/or family [42]. In general, dsRNA mycoviruses persistently infect the host fungus and are transmitted vertically via host cell division, and the infections are usually symptomless.

A large dsRNA in the V670 strain of the violet root rot fungus (*Helicobasidium mompa*) was identified as a hypovirulence factor [43]. The nucleotide sequence of this dsRNA encodes a single long ORF containing conserved RdRp and Hel domains exhibiting significant similarity to those encoded by plant endornaviruses described above, indicating that this large dsRNA virus is a member of the genus *Alphaendornavirus*. The virus was subsequently named *Helicobasidium mompa endornavirus 1* (HmEV1). An increasing number of reports have described endornavirus-like dsRNAs isolated from various phytopathogenic fungi, and nine of them have thus far been recognized as members of the family *Endornaviridae* (Table 1).

Five fungal endornaviruses that infect ascomycetes have shorter genomes (< 10.7 kbp) than alphaendornaviruses and lack the glucosyltransferase domain present in the majority of alphaendornaviruses (Fig. 1), have been classified as members of the genus *Betaendornavirus* (Table 1) [19].

Endornaviruses from other eukaryotic kingdoms

Based on sequence similarities, plant pathogens of the genus *Phytophthora*, an oomycete, have been classified together with diatoms and brown algae into a protist group known as the Stramenopiles. Sequencing and phylogenetic analyses of a large dsRNA from a *Phytophthora* isolate from Douglas fir (*Pseudotsuga menziesii*) revealed that it encodes a single long ORF similar to those encoded by known plant and fungal endornaviruses [44]. This dsRNA virus was recognized as a member of the genus *Alphaendornavirus* and named *Phytophthora endornavirus 1* (PEV1).

Using an *in silico* cloning and bioinformatics approach to obtain full or partial cDNA sequences of genes and comparing them against known dsRNA viral sequences in the NCBI Expressed Sequence Tag database, Liu et al. discovered 119 novel virus-like sequences related to members of the families *Partitiviridae, Totiviridae, Chrysoviridae*, and *Endornaviridae* [45]. They identified one endornavirus-like sequence from the sea louse (*Caligus rogercresseyi*) that exhibited similarity to the fungal endornavirus HmEV1 [45]. As the sea louse is a member of the phylum *Arthropoda*, this finding suggests that endornaviruses are also found in the animal kingdom.

Molecular structures of endornaviruses

Electron microscopic observations revealed that dsRNA genomes of endornaviruses are linear [5, 6]. The dsRNA genomes sequenced to date range from 9760 to 17,635 bp in length and encode a single long ORF of 3181 to 5821 aa residues. This unusually long ORF is one of the unique molecular features of endornaviruses (Fig. 1). Conserved Hel and RdRp domains located in the central and C-terminal regions, respectively, of the long ORF are common features of all endornaviruses described to date (Fig. 1). Other conserved domains found in some, but not all, endornaviruses are viral methyltransferase (MET), glycosyltransferase (GT), and capsular polysaccharide synthetase (CPS) (Fig. 1). In addition, the ORF may encode one or more proteinases that cleave a single long polyprotein into functional proteins, similar to the ORF of potyviruses such as *Potato virus Y*, which encodes a single long polyprotein containing two proteinases [46]. However, putative host-encoded protease(s) might be involved in processing a polyprotein encoded by the ORF of endornaviruses.

Four plant endornaviruses (OsEV, OrEV, VfEV, and BPEV), one fungal endornavirus (HmEV1), and one oomycete endornavirus (PEV1) belonging to the genus *Alphaendornavirus* were shown to contain a site-specific nick in the 5′ region of the coding strand, which divides not only the coding strand but also the single long ORF (Fig. 1) [14, 31, 43, 44, 47, 48]. The biological implications of this nick in the coding strand and the mechanism by which it is generated are unknown. However, because the divided coding strand can no longer be used as a template for noncoding strand synthesis (replication) or mRNA for translation of the polyprotein, the nick must affect at least two important steps in the life cycle of endornaviruses. Therefore, endornavirus dsRNAs containing the nick maybe remain (dead virus bodies) because they have a defect in translation and replication, and the continuous ssRNA of the coding strand may play a vital role in the virus life cycle. However, there are no reports describing isolation of ssRNA molecules of endornaviruses. These two molecular features—the single long ORF and the site-specific nick—have not been reported in other known RNA viruses.

A limited number of reports have demonstrated the functions (or enzymatic activities) of proteins encoded by endornaviruses. RdRp activity was detected in broad bean and rice plants infected with VfEV and OsEV, respectively [49, 50]. Purified cytoplasmic vesicle fractions containing dsRNAs (VfEV or OsEV) exhibited RdRp activity, which requires Mg^{2+} ion and four nucleotide triphosphates. This activity was unaffected by inhibitors of cellular DNA-dependent RNA polymerases (e.g., alpha-amanitin and actinomycin D). Thus, available data regarding the replication of endornaviruses are limited.

Vertical transmission and regulation of copy number in endornaviruses

Although horizontal transmission (infection) of endornaviruses has not been reported, these viruses are often found in a variety of plants. For example, OsEV and BPEV are commonly detected in multiple cultivars of *japonica* rice and bell pepper, respectively [6, 30]. To determine why OsEV is widely distributed in cultivated rice, crossing experiments with OsEV-harboring and OsEV-free rice plants were carried out to examine the vertical (seed) transmission efficiency of OsEV [25]. These experiments demonstrated that the rate of vertical (seed) transmission of OsEV is very high, with transmission via pollen exceeding 98%, whereas that of transmission via ovules was found to be 100% [25]. Although differential centrifugation and sucrose density-gradient centrifugation experiments revealed that OsEV localizes in the cytoplasm of host cells, it is frequently transmitted to progeny plants via both pollen and ovules. The high efficiency of OsEV transmission via both pollen and ovules is likely responsible for the wide distribution of OsEV in many rice cultivars. Thus, the propagation of OsEV (and probably other plant endornaviruses as well) may depend entirely on seed-mediated transmission, and endornaviruses may survive in cooperation with their host plants, indicating that these viruses have a symbiotic rather than parasitic relationship with the host.

OsEV is found in every tissue at every developmental stage in host rice plants. A comparison of the relative amount of OsEV with rice genomic DNA showed that OsEV is maintained at approximately 100 copies per cell [13]. No significant difference in OsEV concentration was found in seedlings, roots, and mature leaves, indicating that a mechanism to regulate copy number may exist in host rice cells. In contrast, the copy number of OsEV in pollen grains was found to be 50-fold higher than in seedlings [14].

The steady replication of endornaviruses before every host cell division (both mitosis and meiosis) and their efficient transmission to the next generation via ovules and pollen are essential for endornavirus propagation because horizontal transmission does not occur. The unregulated increase in endornavirus replication could cause disease or lead to the death of host plants, as occurs with acute virus infections. Conversely, a decrease in copy number could cause the virus to disappear from the host plant (germ cells). The mating of host plants provides an opportunity for endornavirus propagation, so an increase in copy number only in pollen grains is a reasonable strategy to ensure virus transmission, despite their cytoplasmic localization.

Host RNA silencing against endornaviruses

RNA silencing (RNA interference) is the process of sequence-specific posttranscriptional gene silencing triggered by dsRNAs [51–53]. With the exception of mammals, most eukaryotes, such as fungi, insects, and plants, sense exogenous long dsRNAs as viruses and then activate the RNA silencing pathway for defense against virus infection [54, 55]. Extensive studies on the interactions between acute ssRNA viruses and host plants such as *Arabidopsis thaliana* revealed that RNA silencing functions as an innate defense system against acute virus infections in plants. In the RNA silencing pathway, a Dicer or Dicer-like (DCL) endoribonuclease cleaves long dsRNAs into small interfering RNAs (siRNAs) [56, 57], which then associate with an Argonaute (AGO) protein [58]. The siRNA-loaded AGO protein slices specific RNAs exhibiting sequence complementarity between the siRNA and target RNAs [59].

Whereas many plant viruses have ssRNAs as their genomes, their replication intermediates are dsRNAs that trigger activation of the host RNA silencing system (Fig. 3)

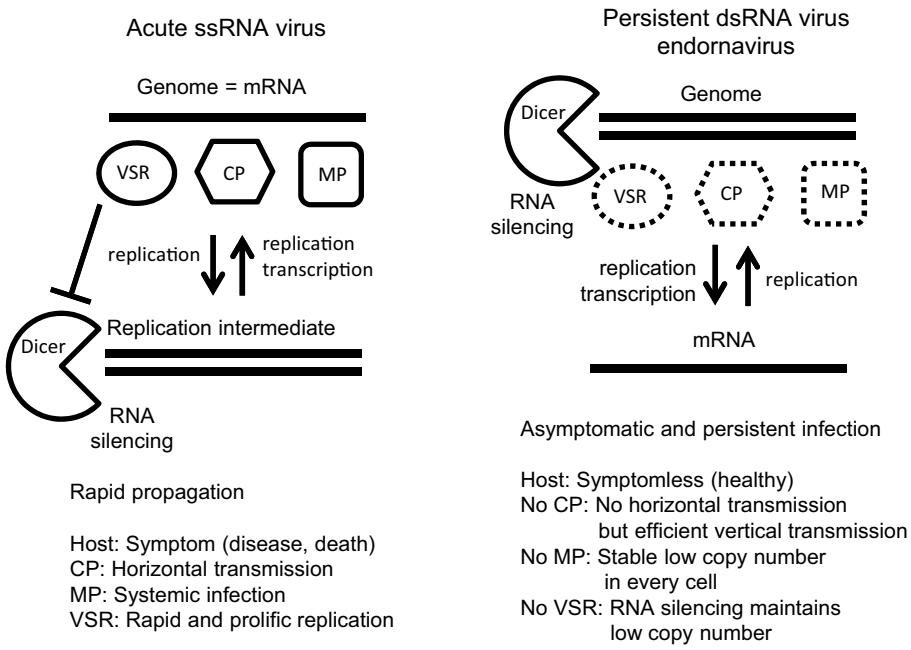

Fig. 3 Comparison of the propagation strategies for persistent dsRNA viruses (endornaviruses) and acute ssRNA viruses

[54, 55]. Therefore, acute ssRNA viruses infect host plants in which 21-nt viral siRNAs (vsiRNAs) generated from their replication intermediate dsRNAs by the activity of Dicer-like 4 (DCL4) accumulate in the host [60–62]. The vsiRNA-loaded AGO proteins then slice the viral genomic ssRNAs [63, 64]. However, many acute ssRNA viruses encode a viral suppressor of RNA silencing (VSR), which inhibits the host RNA silencing system, thus enabling the virus to overcome the host defense system, replicate rapidly in host cells, and propagate systemically in the host plant (Fig. 3) [65–67].

Endornavirus-derived vsiRNAs have been detected in host plants infected with OsEV, BPEV, PvEV1, and PvEV2, indicating that the host RNA silencing machinery recognizes endornaviral dsRNAs [68–70]. The copy number and inheritance of OsEV were examined in transgenic rice plants using a knock-down (KD) construct of genes for the RNA silencing machinery, *OsDCL*s or host RNA-dependent RNA polymerases (*OsRDR*s). A low vertical transmission rate and the disappearance of OsEV during somatic cell divisions were observed in some *OsDCL2*-KD plants, suggesting that KD of a Dicer gene negatively affects the maintenance of OsEV in host plants [68]. The host RNA silencing system may be necessary for persistent infection (symbiotic life cycle) by endornaviruses because it provides for stringent regulation of low copy number (steady replications before every host cell division) and efficient vertical transmission to the next generation (Fig. 3).

Plants, insects, and fungi sense long exogenous dsRNAs as viruses and then activate the RNA silencing pathway [51–53]. In contrast, mammals sense long exogenous dsRNAs as virus infections and respond by activating the immune system because they have specifically developed innate and adaptive immune systems for defense against pathogens [71, 72]. dsRNA viruses in the families *Partitiviridae, Totiviridae, Chrysoviridae*, and *Endornaviridae* are generally associated with symptomless or persistent infections. Although the host range of these viruses includes the four eukaryotic kingdoms (animals, plants, fungi, and protists) [45], they have never been found in mammals [45]. RNA silencing functions as a defense against acute virus infection, but it may also function as a host factor that maintains persistent infections of dsRNA viruses by keeping their copy number low.

Comparison of acute ssRNA viruses and persistent dsRNA viruses (endornaviruses)

Genes encoding replication enzymes such as RdRp, Hel, and Met (a capping enzyme for viral genomic RNAs) are essential for the existence of both acute and persistent RNA viruses. In addition, a capsid (coat) protein (CP), movement protein (MP), and VSR are also essential for the maintenance of acute ssRNA viruses such as TMV and CMV in plants. The CP is essential for viral horizontal transmission from one host plant to another, and the MP is essential for the movement of viruses from one cell to surrounding (neighboring) cells and systemic infection in host plants. VSR also plays an essential role in viral propagation by suppressing the host's defense system (RNA silencing), and in some viruses, a single viral protein exhibits dual CP (or proteinase) and VSR functions [65–67]. Three propagation steps, namely rapid and prolific replication in host cells via

suppression of host RNA silencing by VSR, systemic propagation (infection) within the host plant mediated by MP, and horizontal transmission (infection) from one host to other hosts mediated by CP, constitute a fundamental propagation strategy for acute plant viruses (Fig. 3).

In contrast, endornaviruses have a symbiotic relationship with the host plant. Therefore, even though both CP and MP are essential for the life cycle of acute viruses (systemic infection and horizontal transmission), these proteins are probably not necessary for persistent propagation (i.e., the life cycle) of endornaviruses. Endornaviruses are likely maintained within the host plant for hundreds of generations, suggesting that the host plant regulates virus copy number and propagation and that some host factors control virus replication so that it is coordinated with host cell division. If host plants did not have such factors (proteins), those harboring endornaviruses would exhibit disease symptoms due to unregulated virus propagation, or some of the plant's somatic or germ cells would lose endornaviruses. Therefore, host plants likely express factors that control endornaviruses as symbiont-like parasites. Candidate host factors for regulating persistent dsRNA viruses could be proteins that constitute the RNA silencing machinery. Endornaviruses may employ strategies that enable them to utilize the host RNA silencing and facilitate steady propagation. Indeed, the observation of a low vertical transmission rate and disappearance of OsEV during somatic cell division in *OsDCL2*-KD plants support the above hypothesis [68].

Replication intermediates of ssRNA viruses are dsRNAs, and mRNAs transcribed from dsRNA viruses (endornaviruses) are ssRNAs (Fig. 3). Therefore, both ssRNA and dsRNA viruses have an essentially the same replication cycle, consisting of alternative ssRNA and dsRNA forms, although the duration of each form differs. Acute ssRNA and persistent dsRNA viruses could have evolved from a common ancestor by adopting different propagation strategies: acute ssRNA viruses became independent of the host plant (e.g., they developed rapid replication of their genomic RNA(s) mediated by VSR, systemic propagation in the host plant mediated by MP, and enhanced extracellular stability via encapsulation within CP), but persistent dsRNA viruses developed a highly symbiotic relationship with the host plant (e.g., they developed stringent copy-number regulation and efficient vertical transmission mechanisms). Phylogenetic analyses of viral RdRp and Hel domains encoded by endornaviruses indicate that endornaviruses share a common ancestor with many acute positive-sense ssRNA viruses, such as TMV and CMV [15]. The propagation strategies of acute ssRNA viruses are riskier than those of persistent dsRNA viruses due to development of disease and eventual death of host plants infected with acute viruses. As the propagation strategy of persistent dsRNA viruses (i.e., highly symbiotic relationship with the host plant) may be more advantageous for parasites than that of acute viruses, persistent dsRNA viruses have the broadest host range, encompassing four eukaryotic kingdoms [45]. Acute ssRNA viruses have been extensively studied and are better understood than persistent dsRNA viruses (endornaviruses), but persistent dsRNA viruses are likely more widely distributed in eukaryotes than acute ssRNA viruses. It is likely that many novel viruses discovered in the future will be persistent dsRNA viruses.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

Ethical approval This article does not describe any studies involving human participants or animals.

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