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Complex interactions between insect-borne rice viruses and their vectors

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Insect-borne rice viral diseases are widespread and economically important in many rice-growing countries. Long-term associations between rice viruses and their insect vectors result in evolutionary trade-offs that maintain a balance between the fitness cost of the viral infection of insects and the persistent transmission of the virus by the insect. To promote optimal replication, rice viruses activate innate immune responses, such as autophagy, apoptosis, and stress-regulated signaling pathways in the vector; meanwhile, a conserved insect small interfering RNA antiviral pathway is activated to control excessive viral replication, guaranteeing persistent virus transmission. Furthermore, growing evidence has shown that rice viruses can manipulate their vectors either directly or by inducing changes in host plants to promote the spread of viral pathogens. Thus, understanding the plant–virus–insect relationships offers important insights into how disease epidemics occur and facilitates the design of powerful new strategies for disease control.

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Introduction

In major rice-growing countries, rice viral outbreaks have occurred one after another and inflicted damage on a large scale [1••]. Of the 14 insect-borne viruses known to affect rice, 12 occur in Asia, one in Africa, and one in the American continent [2,3]. The first major rice viral outbreak was recorded in Japan in 1895 for rice dwarf virus (RDV), which was followed by an outbreak of rice stripe virus (RSV) in Japan in 1931 (Table 1) [4,5]. From the mid-1950s to 1980s, 10 insect-borne rice viruses posed serious threats to stable rice production in many rice-growing countries [3]. In the past 20 years, two new rice viruses, southern rice black streaked dwarf virus (SRBSDV) and rice stripe mosaic virus (RSMV), were identified in southern China [6•,7•]. These rice viruses are transmitted by leafhoppers or planthoppers, either in a persistent-propagative or semi-persistent manner [1••,8]. RSV, RDV and rice gall dwarf virus (RGDV) can be transmitted vertically from female insects to offspring in a transovarial manner [9]. Thus, understanding the mechanisms enabling viral transmission by insect vectors is a key component of controlling rice viral diseases in the field. In this review, we summarize recent findings in the interactions between rice viruses and their insect vectors, such as the effects on insect fitness and the role of innate immune responses in viral persistent transmission. In addition, we discuss the role of abiotic and biotic environmental factors in virus–vector interactions in fields, which will likely improve prediction of disease outbreaks and the development of new strategies for disease control by interfering with virus transmission or vector development.

Epidemiological characteristics of vector-borne rice viruses

In general, epidemics of vector-borne rice viruses in the field have three typical characteristics: intermittence, migration and outbreak [1••]. However, the mechanisms that result in such epidemics are still poorly understood. Growing evidence suggests that vector-borne rice viruses, such as RGDV, SRBSDV and RSV exhibit adverse effects on the performance of their adult vectors and the offspring with respect to reducing survival rate, longevity and fecundity [10–12]. Generally, persistent-propagative infection by rice viruses causes a limited adverse, but not pathogenic effect on their vectors. However, these deleterious effects limit the expansion of viruliferous vector populations, thereby restricting the spread of the virus, causing intermittent viral epidemics in the field.

Major outbreaks of vector-borne rice viruses are generally associated with high densities of local overwintering insects or long-distance migration of the vectors [3,8]. How a new vector-borne rice virus emerges and causes an outbreak in the field is poorly understood. RNA viruses usually evolve rapidly, which allows them to escape from

Table 1

Rice virus epidemics and transmission biology

Virus	Year of discovery	Distribution	Family/Genus	Modes of transmission	Vector species
Rice dwarf virus (RDV)	1895	China, Japan, Korea, Nepal, Philippine	*Reoviridae*, *Phytoreovirus*, dsRNA	Persistent, propagative, transovarial	*Nephotettix cincticeps, Recilia dorsalis, Nephotettix virescens, Nephotettix nigropictus*
Rice stripe virus (RSV)	1931	China, Japan, Korea, Ukraine, Siberia	*Phenuiviridae*, *Tenuivirus*, (−)ssRNA	Persistent, propagative, transovarial	*Laodelphax striatellus, Unkanodes albifascia, Unkanodes sapporonus, Terthron albovittatus*
Rice black streaked dwarf virus (RBSDV)	1952	China, Japan, Korea	*Reoviridae*, *Fijivirus*, dsRNA	Persistent, propagative	*Laodelphax striatellus, Ribautodelphax albifascia, Unkanodes sapporona*
Rice hoja blanca virus (RHBV)	1956	Central America	*Phenuiviridae*, *Tenuivirus*, (−)ssRNA	Semi-persistent	*Sesselia pusilla, Chaetocnema pulla, Trichispa sericea*
Rice yellow stunt virus (RYSV)	1965	India, China, Japan, Southeast Asia	*Rhabdoviridae*, *Nucleorhabdovirus*, (−)ssRNA	Persistent, propagative	*Nephotettix cincticeps, Nephotettix virescens, Nephotettix nigropictus*
Rice tungro spherical virus (RTSV)	1965	India, China, Japan, Southeast Asia	*Cecoviridae*, *Waikavirus*, (+) ssRNA	Semi-persistent	*Nephotettix virescens, Nephotettix nigropictus, Nephotettix cincticeps, Nephotettix parvus, Recilia dorsalis*
Rice grassy stunt virus (RGSV)	1966	Southeast Asia, China, Japan	*Phenuiviridae*, *Tenuivirus*, (−)ssRNA	Persistent, propagative	*Nilaparvata lugens, Nilaparvata Muiri, Nilaparvata bakeri*
Rice yellow mottle virus (RYMV)	1970	Africa	*Potyviridae*, *Sobemovirus*, (−) ssRNA	Semi-persistent	*Sesselia pusilla, Chaetocnema pulla, Trichispa sericea*
Rice tungro bacilliform virus (RTBV)	1975	Southeast Asia, India, China	*Caulimoviridae*, *Tungrovirus*, dsDNA	Semi-persistent	*Nephotettix virescens, Nephotettix nigropictus, Nephotettix cincticeps, Nephotettix parvus, Recilia dorsalis*
Rice ragged stunt virus (RRSV)	1977	Southeast Asia, India, China	*Reoviridae*, *Oryzavirus*, dsRNA	Persistent, propagative	*Nilaparvata lugens*
Rice bunchy stunt virus (RBSV)	1980	China	*Reoviridae*, *Phytoreovirus*, dsRNA	Persistent, propagative	*Nephotettix cincticeps, Nephotettix virescens*
Rice gall dwarf virus (RGDV)	1980	China, Japan, Korea, Thailand	*Reoviridae*, *Phytoreovirus*, dsRNA	Persistent, propagative, transovarial	*Nephotettix nigropictus, Nephotettix cincticeps, Recilia dorsalis*
Southern rice black streaked dwarf virus (SRBSDV)	2001	China, Japan, Vietnam	*Reoviridae*, *Fijivirus*, dsRNA	Persistent, propagative	*Sogatella furcifera*
Rice stripe mosaic virus (RSMV)	2015	China	*Rhabdoviridae*, *Cytorhabdovirus*, (−) ssRNA	Persistent, propagative	*Recilia dorsalis*

host immunity and adapt to a new host when cross-species transmission occurs [13]. Thus, viruses with remarkable relative fitness in a given environmental niche may explain the emergence and outbreak of new viral pathogens in different hosts. SRBSDV, the first identified *Sogatella furcifera*-borne reovirus in 2001, and RSMV, the first identified rice cytorhabdovirus transmitted by *Recilia dorsalis* in 2015 (Table 1), have recently spread rapidly throughout southern China [6•,7•]. We deduce that these two rice viruses may have evolved from endogenous virus reservoirs in rice relatives in other plant species, and planthoppers or leafhoppers. The use of deep RNA sequencing would allow monitoring of the emergence of new rice viruses that originated from reservoir hosts. More research is needed on the epidemiology of vector-borne rice viruses in order to implement sustainable management strategies.

Immune response: a burden or a benefit?

Rice viruses are persistently or semi-persistently transmitted by insect vectors with limited harm to the insects, yet they damage plant growth and development [1••].