Research and development status of mycovirus

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Abstract. Mycovirus or fungal virus is a kind of virus that infects fungi and oomycetes and can replicate in them, which widespread in major taxa of fungi and oomycetes. This paper summarized research and development status of mycovirus, including its discovery, classification, transmission, detection techniques, origin and evolution, effects on fungal (oomycete) hosts, interaction with fungal (oomycete) hosts at molecular level and its application in controlling plant fungal (oomycete) diseases, aiming at a basic understanding of the research situation, so as to provide references for mycovirus utilization and future study.

1. Introduction

Using mycoviruses or fungal virus to search the core collection of "Web of Science" database for the past ten years (2010-2019), a total of 2770 papers were found. The titles, abstracts or keywords of these papers included mycoviruses or fungal virus, and the annual publication volume of papers basically shows an increasing trend (Figure. 1). As we know, mycoviruses are a group of viruses that infect and replicate fungi and oomycetes, and are commonly found in fungi and oomycetes of various groups. Many fungal viruses can significantly reduce the pathogenicity of host fungi (oomycetes) after infecting them. Therefore, studying the action mechanism of fungal viruses in host fungi (oomycetes) is of great significance for the control of crop fungal (oomycetes) diseases. At present, certain research results have been obtained in many aspects such as the origin and evolution of fungal viruses, their effects on host fungi, and molecular interactions with host fungi. The research of mycovirus has gradually become a hot area in plant pathology research. Therefore, this article reviews the research overview of mycoviruses in order to provide references for the utilization and further research of mycoviruses.

2. Research status of mycovirus

2.1. Discovery of mycovirus

Most mycoviruses do not cause obvious external symptoms after infection, and only a few fungal viruses can infect the host for a long time and affect it [1]. In 1962, Hollings found three types of viruses (spherical or short sticks) related to the disease through electron microscopy in the cultivated mushrooms [2]. Subsequently, Lampson found a dsRNA virus in *Penicillium funiculosum* [3]. Ellis observed the presence of virions in the culture medium of *Penicillium stoloniferum* by electron microscope [4]. Based on previous studies, Banks found that Penicillium indica virus (PsV) and Penicillium rhizogenes virus (PfV) are both dsRNA viruses [5]. Since then, various fungal viruses have been reported. There have been dozens of reported mycoviruses, about 100 fungi and oomycetes that can be infected by mycoviruses, and they are distributed in more than 50 fungi and oomycetes, some mycoviruses can infect several fungi and oomycetes simultaneously [6].

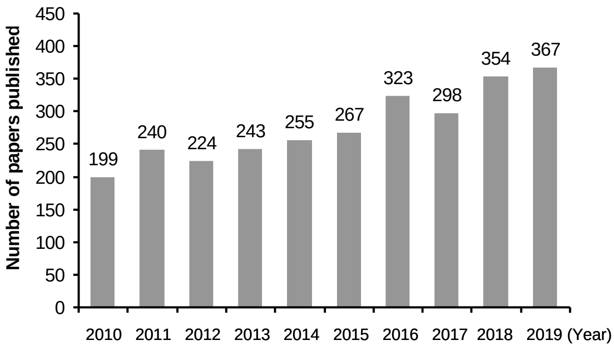

Figure 1. Annual publication volume of papers included mycoviruses or fungal virus.

2.2. *Classification of mycovirus*

Most of the reported mycoviruses are RNA viruses and only a few are DNA viruses. RNA viruses are classified into double-stranded RNA (dsRNA) and single-strande RNA (ssRNA) according to their genome types. Among them, most mycoviruses are dsRNA viruses, and only a few are ssRNA viruses. At present, mycoviruses are mainly divided into 14 families. Among them, 7 families are dsRNA viruses, 5 families are ssRNA viruses, and the remaining 2 families are retroviral RNA viruses. RNA mycoviruses are detailed below (Table 1).

Table 1. Classification of dsRNA mycovirus

Types	Family mambers	Host	Virion shapes
Totiviridae	*Totivirus*	*Sacchromyces cerevisiae* *Rhodotorula* *Ustilago*	Spheroid
	Victorivirus	filamentous fungi	
	Giardiavirus	protozoa	
	Leishmaniavirus	protozoa	
Paritiviridae	*Alphapartitivirus*	filamentous fungi plants	Spheroid
	Betapartitivirus	filamentous fungi	

			plants	
		Gammapartitivirus	filamentous fungi	
Chrysoviridae		*Chrysovirus*	*Penicillium chrysogenum*	Uncoated equidistant spheroid
Reoviridae	*Spinareovirinae*	*Myoreovirus 1* (E.g)	*Cryphonectira parasitica* or *Rosellonia necatrix* etc.	Spheroid
	Sedoorevirinae	*Myoreovirus 2* (E.g) *Myoreovirus 3* (E.g)		
Endornaviridae		*Endornavirus* (E.g)	*Sclerotinia sclerotiorium* (E.g)	-
Megabirnaviridae		*Megabirnavirus*	*Rosellinia necatrix*	-
Quadriviridae		*Quadrivirus*	*Rosellinia necatrix*	-

2.3. Transmission of mycoviruses

Fungal virus transmission is an important part of fungal virus research. Different from animal and plant virus transmission methods, the transmission of fungal viruses is mainly divided into vertical transmission and horizontal transmission. Vertical transmission mainly relies on asexual or sexual spores that carry the virus produced during fungal reproduction. Therefore, spores play an important role in the spread of fungal viruses. Most fungal asexual spores can carry the virus and are easy to spread. Sexual spore-borne virus is not common, and the rate of infection is low. It only occurs in fungi such as *Aspergillus spp.*, *Fusarium spp.*, And *Botrytis cinerea* [7-8].

Under natural conditions, fungal viruses lack an extracellular transmission pathway. Fungal viruses with no spore transmission pathway can be horizontally transmitted in host cells by means of hyphae fusion, so that fungal viruses can migrate from infected cells to healthy cells, but this mode of transmission is limited to strains of vegetative affinity [9-10]. However, some researchers have carried out confrontation cultures on different nutrient affinity groups of *Cryphonectira parasitica* and found that the attenuated virus can be transmitted between different vegetative affinity groups. The efficiency of transmission varies from strain to strain [11]. These studies indicate that vegetative incompatibility is an important obstacle to the spread of low-virulence viruses, but they cannot completely prevent the spread of fungal viruses. At the same time, the limitation of vegetative incompatibility of fungal viruses can also be overcome by artificial techniques. Chen *et al.* [12] successfully introduced the artificial virus full-length sequence into the fungal protoplasts by electric shock, which overcomes the restriction of fungal vegetative incompatibility on the virus transmission. In addition, some researchers have observed the community structure of *Phytophthora infestans* for 4 years and found that the attenuated dsRNA mycoviruses has a natural infection in *Phytophthora infestans* [13].

2.4. Mycoviruses detection technology

Many groups of fungi can be infected by the virus, but not all infected fungi exhibit abnormalities in morphological characteristics. Therefore, it is necessary to determine the presence of fungal viruses through reliable detection techniques. At present, the detection techniques of fungal viruses mainly include electron microscopy, serological methods, enzymatic methods, and various molecular biological technologies.

2.5. Origin and evolution of mycoviruses
There are two hypotheses regarding the origin and evolution of fungal viruses. The first is the co-evolution hypothesis, which assumes that fungal viruses infect fungi from a long time ago and co-evolve as host fungi evolve. The second is the hypothesis of plant virus origin. This hypothesis believes that fungal viruses evolved from the plant-infected process with plant pathogenic fungi in recent times.

The co-evolution hypothesis is because the spread of fungal viruses mainly occurs between cells and rarely occurs at the horizontal level between different hosts. On the other hand, the replication of fungal viruses requires the participation of many host genes. For example, *Helminthos victoria* 190S virus requires enzymes encoded by the host to complete the encapsulation of coat proteins [14]. Other studies have shown that mycoviruses members of the monovirial family and the bivirial family are consistent with their hosts in evolutionary trends. It can be speculated that the mycoviruses of these two families have diversified during the co-evolution process [15].

The hypothesis that fungal viruses originate from plant viruses is that the evolution of fungal viruses and fungal hosts is irrelevant. Some fungal ssRNA viruses are closely related to plant positive-strand RNA viruses, but they are far from related to other fungal viruses. For example, *Botrytis cinerea* virus F and *Sclerotinia sclerotiorium* attenuated RNA viruses are closely related to potato X virus, but they lack coat protein or motile protein compared to plant viruses [16-17].

In addition, some researchers believe that some plant viruses may be derived from fungi. For example, a phylogenetic analysis of diploid virus sequences from plants and fungi has shown that the horizontal transmission of this virus is from fungi to plants [18]. Therefore, it is believed that fungi can be used as vectors for viruses to pass them to plants during the parasitic process of different host plants.

3. Results and discussion

3.1. Effect of mycovirus on host fungi
After the fungal virus infects the host fungus, some fungal viruses form a symbiotic relationship with the host, which has little effect on the host. For example, the researchers studied the effect of dsRNA on the fitness of asexually reproduced *Aspergillus*, and the results showed that the presence of the virus had no significant effect on *Aspergillus*. However, some fungal viruses can cause significant effects on the host after infecting the fungus. This virus is often related to the weak virulence of plant pathogenic fungi, which will cause the pathogenic fungi to decline, symptoms including slowed hypha growth, reduced spore production, and reduced pigment content. For example, a virus consisting of four dsRNA fragments was found on *Alternaria alternata* strain EGS 35-193, which can cause cytoplasmic changes in host fungi. For another example, some researchers found a dsRNA virus

FgV-ch9 on the China-9 strain of *Fusarium graminearum*. The virus causes the mycelium growth of the host fungus to slow down, reduction of spore production capacity, abnormal colony morphology, cytoplasmic disorder and decreased pathogenicity. However, there have been few reports of fungal viruses that cause increased pathogenicity of pathogenic fungi [19-20].

3.2. Molecular interactions between mycovirus and host fungi

Compared with animal and plant virus molecular interaction studies, most fungal viruses lack corresponding reverse genetics methods. Therefore, the molecular interaction research between fungal virus and host fungus is relatively backward. At present, the molecular interaction research between mycovirus and host fungus mainly includes three systems: the interaction system of the attenuated virus CHV1 and *Cryphonectira parasitica*; the interaction system of mycovirus SsDRV and *Sclerotinia sclerotiorum*; the interaction system of fungal virus and *Rosellonia necatrix* [21-22].

3.3. Application of mycoviruses in biological control of plant diseases

Biological control refers to a safe and efficient method for controlling the occurrence and damage of plant diseases by using living organisms or their metabolites. At present, the application of fungal viruses in biocontrol of plant diseases is mainly carried out through three mechanisms, namely the production of attenuated strains, and the lethal or protective effects of metabolites on pathogenic fungi [23-24].

At present, in the field of fungal virus research, researchers have tried to study the spread of fungal viruses, the regulatory mechanism, the replication mechanism, and the molecular interaction mechanism between fungal viruses and host fungi at the molecular level. However, due to the constraints, a lot of work has just begun. With the continuous development and improvement of technologies such as reverse genetics, bioinformatics, and high-throughput sequencing, the problems encountered in the research of fungal viruses will hopefully be solved. At the same time, we know that fungal viruses are widely distributed in major fungal and oomycete groups, and some fungal viruses can cause the pathogenicity of plant pathogenic fungi and oomycetes to decline. There is already sufficient evidence that fungal viruses are associated with a weakly virulent phenotype in *Sclerotinia sclerotiorum*, *Botrytis cinerea* and so on. From the perspective of crop protection, fungal viruses are beneficial to the sustainable development of agriculture as a means of biocontrol. In addition, the research on the interaction between virus and host is the main field of modern virology research, and the interaction between fungal virus and host fungus can be used as a model to explore the effect of mycovirus on host fungus. Therefore, screening and studying the interaction mechanism between this type of fungal virus and host fungus will open new ways for the application of fungal viruses in biological control [25].

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