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A COMPREHENSIVE REVIEW ON MYCOVIRUSES AS BIOLOGICAL CONTROL AGENT

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ABSTRACT

Mycoviruses are viruses that infect fungi. They have been reported in all major taxa of fungi. Generally extracellular phase is not present in mycoviruses and are transmitted during cell division intracellularly in sporogenesis, and/or hyphal anastomosis. The genome of mycoviruses has dsRNA, but a number of positive- or negative-strand ssRNA and ssDNA viruses have been isolated and characterized. There is an increasing interest for use of mycoviruses as novel biocontrol agent as they reduce the virulence of their phytopathogeinc fungal hosts. Mycoviruses can also infect endophytic fungi and encode killer toxins. Better understanding of mycoviruses assembly, function, and evolution have been done through their structural analyses. Recent report on virus taxonomy suggested that mycoviruses genome mostly consists of double-stranded RNA (dsRNA), and about 30% of mycoviruses genome is composed of a positive, single-stranded RNA (+ssRNA). Recently a mycovirus that is related to Gemini viruses has been reported. Scientists have reported mycoviruses in *Chytridiomycota, Zygomycota*, *Ascomycota, Deuteromycota*, and *Basidiomycota*. Many mycoviruses and their fungal hosts still remain unknown recently developed metagenomics approaches will be useful for detecting and identifying new mycoviruses.

Key word: Mycoviruses, hypersensitivity, biological control, *Agaricus bisporus, Aspergillus foetidus*.

INTRODUCTION

A virus that infects and replicates in fungi is known as mycovirus or mycophages. They are often typically latent but some induce symptoms. They are present in all taxonomic groups of fungi. Very few information is known about the mycoviruses of the lower fungi. During 1950s, several disorders in fungi were described and some authors suspected for the involvement of viruses. In 1962 first evidence was given of viruses that infected the cultivated mushrooms, *Agaricus bisporus* causing die back disease. The mushroom virus diseases are the major cause of crop loss and the degeneration of mycelium in the compost (Suman and Sharma, 2007).

Most of the mycoviruses cause latent infections; however, several mycoviruses are involved in hypo virulence, and can be used as biocontrol agent to control fungal diseases of economic importance. For this reason, psychopathologists are interested in studying the mycovirus mediated hypo virulence in plant pathogenic fungi. Molecular properties of mycoviruses can be helpful to understand the virus fungal interaction and ecology and evolution of viruses. These findings can be used as molecular basis of fungal pathogenicity (Romaine and Schlagnhaufer, 1995; Yu *et al.*, 2010). The genome of mycoviruses mostly consists of double stranded RNA (dsRNA) and positive ssRNA but a few mycoviruses with negative single-stranded RNA (ssRNAs) and DNA (ssDNA) genomes have been reported., mycoviruses having ssRNA genome are taxonomically classified into seven families, *Alphaflexiviridae, Barnaviridae, Endornaviridae, Gammaflexiviridae, Hypoviridae, Narnaviridae*, and "*Fusariviridae*" (Bozarth, 1972; King *et al.*, 2011).

History of mycoviruses: The first economically important mycoviruses was discovered in the late 1940s in La France disease of cultivated mushrooms (*Agaricus bisporus*) (Hollings, 1962). General symptoms of this disease include watery stripe, waterlogging, slow mycelial growth, dieback, malformation, premature maturation, reduced shelf life and reduced yield.

Model organism used for studying hypo virulence in fungi is *Cryphonectria parasitica* hypovirus 1 (CHV1). It had been successfully used in Europe to control chestnut blight fungus. It has small number of vegetative compatibility groups (VCGs). 35 VCGs have been found in USA (Anagnostakis *et al.*, 1998), while in China and Japan 71 VCGs have been identified so far (Liu and Milgroom, 2007).

The occurrence of mycoviruses: The presence of mycoviruses has been reported from all major taxonomic groups of fungi. Almost fifty five mycoviruses has been observed in forty four genera and fifty six different species of fungi (Pearson *et al.*, 2009). Random sampling of fungus cultures has indicated that 10 to 15% of the species contain mycoviruses and there is good reason to believe that a virus can be found in any species with diligent searching. Some-important fungi containing mycoviruses are *Agaricus bisporus* (25-50 nm*), Alternaria tenuis* (30-40 nm), *Aspergillus foetidus* (40-42 nm), *A. glaucus* (25 nm), *A. niger* (40-42 nm). *Penicillium brevicompactum* (40 nm) *P. chrysogenum* (35 nm), *P. funiculosum* (25-30 nm) *P. notatum* (25 nm), *P. stoioniferum* (40-45 nm), *Peziza ostrachoderma* (17 x 350 nm), *Endothiaparasitica* (300 nm), *Laccaria laccata* (28 nm), *Stemphilium botryosum* (25 nm; VLPs), *Saccharomyces cerevisiae* (40 nm) etc (Pearson *et al.*, 2009).

Types of mycoviruses: So far, only small number of mycoviruses has been characterized, and most of them are only the 'virus like particles' (VLPs) in electron micrograph of partially purified extracts from the fungus or sometimes from thin section studies. Several different morphological types of VLPs have been observed, some corresponding fairly close with well known viruses of the other host taxa. Some of the examples of mycoviruses are given in (table 1).

Table 1: Virus particles reported in fungi.

(http://www.biologydiscussion.com)

Fungal species	*Virion size (nm)*
Agaricus bisporus	25-50.19-50 (rods)
A. compestris	25-50.19x50 (rods)
Alternaria tenuis	30-40
Aspergillus foetidus	40-42
A. glaucus	25
A. niger	40-42
Endothia parasitica	300. club shaped
Gaeumannomyces tritici	29
Laccaria laccata	28
Penicillium brevicompactum	40
P. chrysogenum	35
P. funiculosum	25-30
P. notatum	25
P. stoloniferum	40-45
Peziza ostracoderma	17x350 (rods)
Stemphilium botryosum	25.VLPs
Saccharomyces cerevisiae	40

Mycoviruses recorded so far show morphologically variable forms, viz., bacilliform, rod- shaped, filamentous and herpes types (Pearson *et al.*, 2009). But majority of the known mycoviruses are typically isodiametric ranging usually from 25 and 50 nm in diameter and particle weight from 6-13 x 10^6 dalton. The most outstanding feature common to mycoviruses is possession of double-stranded ribonucleic acid (dsRNA) usually segmented into 1-8 segments with a total molecular weight of 2 to 8.5 x 10^6 dalton.

The dsRNA segments are separately enclosed into identical capsids. This feature of mycoviruses differentiates them from plant and animal dsRNA viruses in which the genetic material segments are, usually, all enclosed in a single virion. Some of the isometric particles (105-110 nm diameter) i.e. viruses containing capsid roughly spherical polyhedron, superficially resemble iridoviruses, and some others (about 50 nm diameter) resemble caulimoviruses. Tailed DNA phage particles and paired 20 nm isometric particles of possibly Gemini virus type have also been reported. Most of the virus particles recorded in fungi has been isometric with a genome of several specie (Buck, 2017).

Taxonomy of mycoviruses: Mycoviruses have double-stranded RNA (dsRNA) genome, about 30% have positive sense, single-stranded RNA (+ssRNA) genomes (Bozarth, 1972) (Pearson *et al.*, 2009) and only one of a single-stranded DNA (ssDNA) mycovirus is known. In *Sclerotinia sclerotiorum* a Gemini virus has been found that causes hypo virulence to its host (Yu *et al.*, 2010). 10 viral families with 90 mycoviruses species have been identified. As the morphology of mycoviruses is concerned, they mostly exist in isometric forms. It is impossible to investigate new families and genera of mycoviruses because of lack of genomic data. 'Mycovirus sphere' is dominating in different viruses of the families *Narnaviridae* , *Partitiviridae* and *Totiviridae* .

Origin and Evolution: It is still clearly not understandable how viruses originated. According to the recent data viruses have emerged from 'super groups' of eukaryotes in a very early stage of life on earth. Evidence have shown RNA viruses' first colonized eukaryotes and co-evolved with their hosts. This concept of evolution fits well with the 'ancient co-evolution hypotheses. The diversity of mycoviruses can be explained by this hypothesis (Varga *et al.*, 2003; Forterre, 2006).

During evolution process plant viruses introduced extracellular phase into life cycle of mycoviruses because they have movement proteins. After the recent discovery of an ssDNA mycovirus, it has been suggested that DNA and RNA viruses have a common evolutionary mechanism. Although in many cases mycoviruses are group with plant viruses. Phylogenetic relatedness of CHV1 (which confer hypo virulence) to *Potyvirus* gene with the ssRNA genome (Koonin and Wolf, 2008) and also some viruses have often found closely related to the plant viruses than other groups of mycoviruses (Pearson *et al.*, 2009). Therefore due to this fact another question rises about the movement of these viruses from plant host to fungal pathogenic host. This theory can be helpful to understand how mycoviruses evolve further.

Host Range and Incidence: Mycoviruses are reported to be found in *Chytridiomycota, Ascomycota*, *Basidiomycota* and *Zygomycota*. There are reports on the infection of fungi with more than two non-host viruses with dsRNA defects and dsRNA satellite (Howitt *et al.*, 2006). Viruses that are distinct from mycoviruses have also been found as, they cannot reproduce in the fungal cytoplasm but they use fungi as vectors (Adams, 1991). Host range of the mycoviruses are limited to vegetative compatible groups that allow cytoplasmic fusion (Buck, 2017), but the replication of mycovirus in some other taxonomically variable non-host fungi (Ghabrial and Suzuki, 2009). Two fungal species *Sclerotinia homoeocarpa* and *Ophiostoma novo-ulmi* as host for mycoviruses has been reported (Deng *et al.*, 2003). It is possible to extend the natural host range of *Cryphonectria parasitica* hypovirus 1 (CHV1) to several fungal species that are closely related to *C. parasitica* using in vitro virus transfection techniques (Chen *et al.*, 1994). CHV1 can also propagate in the genera *Endothia* and *Valsa* (Dawe and Nuss, 2001), which belong to the two distinct families *Diaporthaceae* and *Cryphonectriaceae* individually.

Transmission of mycoviruses: During cell division mycoviruses move intracellularly or via hyphal fusion because of absence of genes for 'cell-to-cell movement' proteins. Mycoviruses may have many routes of infection like,

plasmogamy, production of large amount of sexual spores, cytoplasmic exchange, overwintering via sclerotia; transmission into sexual spores' therefore external route of infection is not needed by mycoviruses. The potential barriers to mycovirus spread could be Vegetative incompatibility and variable transmission of sexual spores. Depending on the virus-host combination the rate of transmission of spores through sexual reproduction can be 0% to 100%. Inter and interspecies transmission of these mycoviruses had also been reported previously comprises of *Cryphonectria*, *Sclerotinia* and *Ophistoma* (Ghabrial, 1994; Liu *et al.*, 2009). Intraspecies transmission among isolates of black *Aspergillus* and *Fusarium poa* has also been reported (Van Diepeningen *et al.*, 2006).

The exact mechanism by which the fungi overcome the physical and genetic barriers are still unknown, it may be due to the recognition process of host during physical contact or other ways of spread *i.e.,* vectors. Hosts viral infection status plays an important role in transmission, whether it is infected with same or different virus. It has also been reported that mycoviruses has an important role in secondary mycoviral infection regulation. Extracellular transmission of mycoviruses is often missing because in the infectious life cycle of all viruses crossing the cellular membrane is a key step. Rigid cell wall of fungi serves as a barrier to extracellular virus uptake because of the large size of the dsRNA mycoviruses as compared to the cell wall pores. In case of Intracellular transmission of mycoviruses may be horizontally (protoplasmic fusion) and vertically (sporulation). Horizontal transmission occurs through the hyphal fusion and cell division. While vertical transmission is through asexual or sexual spore (Van Diepeningen *et al.*, 1997). According to the researchers mycoviruses are not classified as true viruses unless they possess the transmission evidence (Vijay and Sunita, 2016).

Symptoms associated with mycoviruses: Cryptic or latent (symptomless) infections are caused by mycoviruses. Mycoviruses can change morphology of the fungus such as change in colony morphology, pigmentation, reduced growth, and lack of sporulation, attenuation of virulence in their host. Phenotypic effects may include hypo virulence or killer phenomena in their host. Reduced growth rate, reduced pigmentation, reduced asexual sporulation, loss of fertility are major characteristics of hypo virulence (Van Diepeningen *et al.*, 2006; Deng *et al.*, 2007). The ssRNA or, dsRNA genomes are involved in hypo virulence. While in case of the killer phenomena proteins encoded by satellite dsRNA are involved. Biological control of mycoviruses that can weaken the infection caused by pathogenicity of fungi is of great interest for researchers. Some mycoviruses that have been isolated from filamentous fungus excrete Killer toxin (Adams, 1991). On the other hand, certain distinctive group of mycoviruses are beneficial to their hosts (Buck, 2017). Some beneficial effects of mycovirus on their host have been reported as mycovirus with endophytic fungus *Curvularia protuberata*, panic grass *Dichanthelium lanuginosum* improve the ability to survive in harsh environmental conditions such as high temperature (Deng *et al.*, 2003). Some CHV1 hypo virus isolates (CHV1-Euro7 and CHV1-EP713) had high sequence identities that cause the specific distinct symptoms (Schmitt *et al.*, 1997).

The mechanism of infection and transmission of mycoviruses is still obscure. They have been found in fungal spores and it is believed that they are transmitted through the spores. The presence of viral-RNA in the fungal cells does not appear to affect any cellular properties such as antibiotic production (Iwasaki and Medzhitov, 2015). For example *Penicillium notation* contains a dsRNA mycovirus, but penicillin production by the fungus is not affected at all. In recent years the dsRNA mycoviruses have attracted the attention of scientists since they have ability to induce interferon production in animal cells. Also, they do not appear to the animal cells be toxic unlike other chemicals that induce interferon production.

The killer phenomenon of mycoviruses: In recent years, much emphasis has been laid on the production of 'killer toxin' and mycovirus dsRNA segment. Some strains of *S. cerevisiae* and *Ustilago maydis* (com smut fungus) secrete extracellular toxins that either kill or suppress the growth of same or related fungal species but each killer strain is immune to its own toxin (Brown and Hammond-Kosack, 2015). The most sensitive race of *S. cerevisiae* contains the viral particles of 40 nm diameter with a single dsRNA designated as L. The Killer strains also contain a dsRNA of molecular weight of about 1.1 – 1.4 × 10^6 designated as M (Özkan, 2014). The coat proteins of both are indistinguishable serologically or in electrophoresis. The M dsRNA encodes the labile glycoprotein killer strain (confirmed by in vivo translation) and is believed to determine the immunity factor. The M is found only in cells containing the L dsRNA. The L is supposed to encode both RNA polymerase and the coat protein for L and M RNAs.

Mycoviruses as biocontrol agents: Majority of plant diseases are caused by fungal pathogens. Use of fungicides is a common practice to control fungal phytopathogeinc diseases. Fungicide-resistant strains are developed by Continuous use of fungicides; it also causes potential hazardous effects to the humans and environment. In recent year's use of biocontrol agents as an alternative to the chemical control has gained much importance. Also mycoviruses have the potential to be used as biocontrol agents. Nuss (1992) first demonstrated the ability of a dsRNA virus as a biocontrol agent against the chestnut blight. Construction of cDNA copy of hypovirus associated viral RNA and transformed it into the fungal virulent strain which converted the compatible, virulent strain to a hypo virulent strain. In Europe CHV-1 cDNA was successfully used to control chestnut fungus but in North America fungus showed greater genetic diversity and failed to control the disease (Nuss, 1992). Transmission of the viruses through hyphal interaction causes restrictions for their successful transmission.

Hypo virulence is the advantageous infection of viruses which decrease the pathogenicity of plant pathogenic fungi. In simple words a reduction in disease producing capacity of the pathogen. Hypo virulence is the most common in mycoviruses and used for biological control of various plant diseases such as *Cryphonecteria parasitica* (chestnut blight), white root rot of woody plants, rice blast and against various soil borne pathogens (Zhang and Nuss, 2016).

The mechanism of hypo virulence is still not clear, but various hypothesis were given by different workers, such as signal transduction pathways =, RNA silencing of the fungus and the counter silencing mechanisms by the hypovirus (Nuss, 2011). There are various other mechanisms, which are reported such as mitochondrial mutations, nuclear mutations and plasmids have been, or may be, associated with hypo virulence. The development of cDNA infectious clone and other transformation techniques (Chen *et al.*, 1994), extend the host range of mycoviruses, without the obstacles of vegetative incompatibility.

Beneficial interactions: Studies have shown that apart from causing hypo virulent interactions mycoviruses also caused beneficial effects. Killer strain of fungi that are encoded with proteinaceous chemicals contains dsRNA elements to which the host is immune, but it cause lethal effects on the fungal strain that do not produce toxin. Basic advantage that host get through theses mycovirus is the complete elimination of competitors growing in the same environmental condition. A three way symbiosis between a mycovirus, the endophytic fungus (*Curvularia protuberata*), and panic grass (*Dichanthelium lanuginosum*) have been described by Márquez *et al.* (2007). Infection by a dsRNA virus enables fungus and the plant to tolerate high temperatures. It has been observed that infected and un infected cultures of *Botrytis* showed significant differences in in vitro growth rates in response to mycovirus so the infected culture grow fast as compared to non-infected ones (Tan *et al.*, 2007).

The future prospects: Non-symptomatic nature of mycoviruses and lack of infectivity has make study of mycoviruses very challenging. In coming years new tools of will be available by advancement in molecular biology, which will be very useful to study mycoviruses (Fillinger and Elad, 2016). It will be easy to discover virus-host by interactions, using full genomic sequence of target hosts, *i.e. A. bisporus, B. cinerea and S. sclerotiorum* (Göker *et al.*, 2011). Control of plant pathogens by mycoviruses as a biocontrol agent is the most promising area of research. For this purpose the knowledge of both host and virus behavior in the field is very important. Knowledge Understanding of population biology of mycoviruses is also important as that of fungi to expand biocontrol opportunities of mycoviruses (Pearson *et al.*, 2009). Detail of mycoviruses their fungal plant hosts is described in (Table 2).

Table 2: Details of mycoviruses and their fungal plant hosts along with symptoms.

Mycoviruses	Fungi	Fungal Host	Symptoms	Viral genome type	References
FgV1-DK21	*F. graminearum* isolate DK21	Barley, Maize, (Korea)		dsRNA (1segment)	Cho *et al.* (2013)
FgV2	*F .graminearum* isolate 98-8-60	Barley (Korea)		dsRNA1, dsRNA2, dsRNA3, dsRNA4, dsRNA5,	Cho *et al.* (2013)
FgV3	*F. graminearum* DK3			dsRNA	Cho *et al.* (2013)
FgV4	*F. graminearum* isolate DK3		Reduced	dsRNA1, dsRNA2	Cho *et al.* (2013)
FgV-ch9	*F. graminearum* isolate china9	Cereals (China)	mycelia growth,	dsRNA1, dsRNA2, dsRNA3, dsRNA4, dsRNA5,	Cho *et al.* (2013)
FpV1	*F .poae*	Wheat	increased	dsRNA1, dsRNA2, (VLP)	Cho *et al.* (2013)
FoVI	*F. oxysporum*, *f.*sp.*melonis*		pigmentation	dsRNA1, dsRNA2, dsRNA3	Cho *et al.* (2013)
FsVI	*F. solani*, *f.*sp.*robiniae*			dsRNA1, dsRNA2	Cho *et al.* (2013)
PdV1	*P. digitatum* strain HS-RH1	Citrus fruit	Reduced	dsRNA	
VdPV1 (*Verticillium dahliae* partivirus 1)	*Verticillium dahliae* Vd08284	Cotton, potato, soybean, tomato and beet	mycelial growth, smaller colony size	dsRNA1 dsRNA2	Feng *et al.* (2013)
RsRV-HN008	*Rhizoctonia solani*	Rice (China)	on PDA	dsRNA	Zhong *et al.* (2015)
NoNRV1 (Nigrospora oryzae no segmented RNA virus1	*Nigrospora oryzae*	Maize, rice, Sorghum, cotton, weeds, kentucky, blue grass, Brown mustard, alovera	medium and hypo virulence	Non segmented RNAvirus	Zhong *et al.* (2015)
SsHADV-1 (*Sclerotinia sclerotiorum* hypovirulence associated DNA virus1)	*Sclerotinia sclerotiorum* (hypovirulent strain DT-8)	rapeseed, soybean, sunflower and numerous vegetables	Hypo virulence	ssDNA	Yu *et al.* (2013)

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