

A REVIEW

Mycoviruses and their role in biological control of plant diseases

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SUMMARY

Mycoviruses are the viruses that infect fungi and prevalent in all major groups of plant pathogenic and edible fungi. The first mycovirus was reported in 1962 from the cultivated mushroom (*Agaricus bisporus*); the infected mushrooms developed malformed fruiting bodies, grow slowly, mature early and resulting in serious yield losses. Although the majority of known mycoviruses have dsRNA genomes that are packaged in isometric particles, but there are also some reports of DNA mycoviruses. These are transmitted intracellularly during cell division, sporogenesis and cell fusion, but apparently lack an extracellular route for infection. Their natural host ranges are restricted to individuals within the same or closely related vegetative compatibility groups. Mycoviruses causes debilitating diseases of mushrooms; reduce the virulence of their phytopathogenic fungal hosts, production of killer proteins and increase the thermal tolerance of infected host plant. These fungal-virus systems are precious for the development of novel biocontrol strategies. Hypovirulence associated mycoviruses and killer yeast to control plant diseases is emerging as one of the latest biological tool.

Key Words : Mycoviruses, dsRNA, Hypovirulence, Killer yeast

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The viruses that infect fungi and multiples within the fungi are called mycoviruses. They are also known as fungal virus, mycophage and virus like particles (VLPs). The majority of mycoviruses have segmented double-stranded RNA (dsRNA) genomes (Ghabrial, 1994); however, a DNA virus was recently identified from the fungal plant pathogen *Sclerotinia*

sclerotiorum, which suggests that fungi may host both RNA viruses and DNA viruses (Xie *et al.*, 2006; Liu *et al.*, 2009; Liu *et al.*, 2010; Yu *et al.*, 2010 and Xie *et al.*, 2011). Mycoviruses have isometric particles, approximately 30 per cent have positive sense, and single-stranded RNA (+ ssRNA) genome and they must have the ability to be transmitted, in other words they are able to infect other healthy fungi. Significant difference between the genomes of mycoviruses to other viruses is the absence of genes for cell to cell movement proteins (Sinha and Tarafdar, 2007; Kotakadi *et al.*, 2012). Mycoviruses are typically grouped into several families, including Totiviridae, Partitiviridae, Chrysoviridae, Hypoviridae and Nanoviridae. Although the families of many mycoviruses cannot be determined, they are

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phylogenetically related to typical plant viruses and even to animal viruses. Mycoviruses infect the fungi in phylum Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota. Therefore, mycoviruses can move only intercellularly during cell division or via hyphal fusion. There are two major hypothesis which have been proposed to explain the origin of mycoviruses. Ancient coevolution hypothesis states that although the origin of mycoviruses is unknown, the association between mycoviruses and fungi is ancient and reflects long-term coevolution. Plant virus hypothesis, suggests that mycoviruses originated relatively recently from plant viruses; i.e., the original mycovirus was a plant virus that moved from plant to fungus within the same host plant (Pearson *et al.*, 2009). Similar scenarios might also explain the origin of plant viruses; i.e., some plant viruses may have originated from mycoviruses that moved from fungus to plant. Because convincing data are lacking, however, the origin of mycoviruses remains a mystery. Mycoviruses have been isolated from various fungi, including mushrooms, medical fungi and plant pathogenic fungi, and are believed to commonly exist in fungi. First mycovirus was reported by Hollings in 1962 on diseased mushrooms sporophores that were later known as La France disease or watery stripe disease of mushroom. During 1970s, hypovirulence in chestnut blight (*Cryphonectria parasitica*) led to the discovery of mycoviruses in plant pathogenic fungi. Presence of mycoviruses in fungi can be detected by the symptom produced on the infected fungi, comparative growth rates of the mycelium on agar, direct electron-microscopic examination (EM), immunosorbent electronmicroscopy (ISEM), polyacrylamide gel electrophoresis (PAGE), enzyme-linked immunosorbent assay (ELISA) and reverse transcription polymerase chain reaction assay (RT-PCR). Various mycoviruses have been shown to mediate reduced virulence (hypovirulence) in their plant pathogenic hosts e.g. hypovirus (CHV1) of the chestnut blight, *Diaporthe ambigua* (DaRV), *Rhizoctonia solani* (*Rhizoctonia* virus M2) and *Magnaporthe oryzae* (MoV1 and MoV2). Mycoviruses are able to produce the killer proteins that are lethal to the other closely related or same species fungi. This phenomenon was earlier known as the killer yeast, assumed as the genetic phenomenon of the fungi, but later with advancement; it is believed that this is due the presence of the dsRNA viruses. Mycoviruses also increases the fungal host tolerance to the high temperature. Isolation, production,

purity and stability of mycoviruses still remain the untouched area and much more work is to be done in near future to reveal out the complete information. It has been a half century since the first mycovirus was discovered and mycoviruses remain attractive because of their importance in the biological control of fungal plant diseases and its beneficial effects to fungal host plant.

Symptoms associated with mycoviruses :

Mycoviruses can alter phenotypes of infected fungi, such as reduced growth, pigmentation and lack of sporulation. They cause change in morphology, colony of infected fungi and cause latent and persistent infections (Buck, 1986). Some mycovirus families are connected with variable phenotypic effects such as hypovirulence or killer phenomena in their host. Hypovirulence is, among other characteristics, defined as reduced pigmentation, reduced asexual sporulation, loss of fertility and reduced growth rate (Van Diepeningen *et al.*, 2006; Polashock *et al.*, 1997; Park *et al.*, 2004; Deng *et al.*, 2007; Jiang and Ghabrial, 2004). Hypovirulence associated mycoviruses have ssRNA or, mainly, dsRNA genomes. The killer phenomena are induced by proteins encoded by satellite dsRNA (Schmitt *et al.*, 1997).

Transmission of mycoviruses :

Mycoviruses often lack the extracellular transmission because crossing the cellular membrane is a key step in the infectious life cycle of all viruses. It is understandable that the rigid cell wall in fungi serves as a membrane shielding structure constituting a barrier to extracellular virus uptake. As the dsRNA mycoviruses are larger in size than the pores of the cell wall, thus, prevents the virus entry inside the cell. Consequently, mycoviruses are unable to initiate fungal infections by extracellular transmission. Infection by the extracellular transmission could thus, far only be achieved in special experimental settings using protoplasts (Yphantis *et al.*, 1967). Intracellular transmission of mycoviruses is mainly by two ways, horizontally via protoplasmic fusion (anastomosis) and vertically by sporulation. Horizontal transmission only through the hyphal fusion and cell division. Vegetative incompatibility reactions inhibit hyphal fusion and reduce viral transmission. In septate fungi, hyphal compartments are interconnected through hyphal pores. Replicating mycoviruses are thus, able to spread throughout the mycelium/hyphae cytoplasmic streaming. As a rule, however, when two fusing hyphae are not

compatible, they recognize each other as nonself, which triggers programmed cell death (PCD).

In Aspergilli, the genes involved in activation of PCD reactions are currently being characterised and regarded as a promising approach to combat invasive Aspergillosis transmission of mycoviruses fails in case which genetic incompatibility is mostly followed by death of the hyphal fusion cell, the so-called heterokaryon, and often of surrounding cells (Fedorova *et al.*, 2005; Davies *et al.*, 2004; Fedorova *et al.*, 2008; Van *et al.*, 2009). Mycoviruses are mainly spread by vertical intracellular transmission through asexual or sexual spore formation, with asexual sporulation being the most efficient means of transmission (Coenen *et al.*, 1997; Hillman and Suzuki, 2004; Van Diepeningen *et al.*, 1997 and Liu *et al.*, 2003).

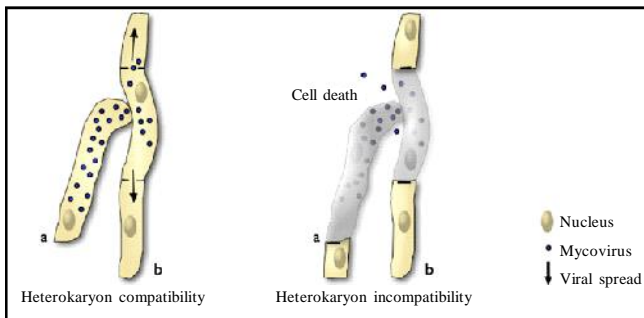


Fig. 1 : fusion cell

Mycoviruses infects various mushrooms :

Mycoviruses are both harmful and beneficial. First mycovirus was identified by Hollings in 1962 on diseased mushrooms sporophores. Mycoviruses are harmful, when they are infecting the mushroom and cause the various diseases of mushrooms such as La France disease and browning etc. Mycoviruses causes reduction in yield, slow mycelial growth, water logging of tissue, malformation, miss sharpened mushroom and reduces the market value of the mushrooms. Borodynko *et al.* (2010) studied La France disease of the cultivated mushroom *Agaricus bisporus* in Poland. He concluded that La France disease was caused by dsRNA virus i.e. La France isometric virus (LFIV) and exhibiting a wide range of the disease symptoms including premature veil opening, brown coloured mushrooms, and loss of crop yield. Similarly, the brown discoloration of fruiting body of *Flammulina velutipes* caused by a mycovirus *F. velutipes* browning virus (FvBV); which reduces the market value of the mushroom (Magae and Sunagawa, 2010).

Hypovirulence :

Hypovirulence 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. Hypovirulence is the most common in mycoviruses and used for biological control of various plant diseases such as *Cryphonectria parasitica* (chestnut blight), white root rot of woody plants, rice blast and against various soil borne pathogens.

Mechanisms of hypovirulence :

The mechanism of hypovirulence is still not clear, but various hypothesis were given by different workers, such as signal transduction pathways (Turina and Rostagno, 2007), 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 hypovirulence.

Hypovirulence against *Cryphonectria parasitica* (Chestnut blight) :

Chestnut blight cankers were first reported in the United States in 1904 on American chestnut trees. In 1926 the fungus was reported throughout the native range of American chestnut. In 1913, Frank Meyer also reported the disease in China and in 1915 from Japan. After its discovery in 1904, the blight spread rapidly at about 20-50 miles per year. By 1950, the blight had devastated 9 million acres of forests by killing several billion American chestnut trees. Jene Grente reported in 1965 'hypovirulent' strains of the blight fungus from Italy and use of these strains in a successful biological control of chestnut blight. After four or five years of therapy, hypovirulent strains began to spread through the chestnut orchards of France, the trees began 'healing' over the blight cankers with bark-callus tissue. In 1972, Grente's hypovirulent strains were imported to USA and used as biocontrol agent.

Hypovirulence against *Rhizoctonia solani* (Sheath Blight of rice) :

Strain GD-11 of *R. solani* AG-1 IA causing sheath blight of rice having dsRNA mycovirus *Rhizoctonia solani* partitivirus 2 (RsPV2). The RsPV2 genome comprises two dsRNAs and mycoviruses RsPV2 shows a high sequence identity with the members of genus

Alphapartitivirus in the family Partitiviridae. When the purified RsPV2 virus particles introduced into protoplasts of a virus-free virulent strain GD-118 of *R. solani* AG-1 IA resulted in a derivative isogenic strain GD-118T with reduced mycelial growth and hypovirulence to rice leaves. Therefore, the novel dsRNA virus can be used successfully in biological control of *R. solani* (Zheng *et al.*, 2014).

Hypovirulence against *Fusarium graminearum* :

Fusarium graminearum isolates China-9 evaluated against the dsRNA mycovirus FgV-ch9 for hypovirulence-related traits. Single conidial originating cultures of China-9 isolate can be associated either with high, medium or low amounts of the viral dsRNAs. At high and medium dsRNA levels, China-9 isolates exhibit reduced mycelia growth rate and conidiation capacity, abnormal colony morphology, disorganized cytoplasm, as well as reduced virulence for wheat and maize plants. At low dsRNA levels the fungus shows no symptoms, however, the RNA segments can be detected by RT-PCR. Transfection of the virulent *F. graminearum* PH-1 isolate with purified Virus-like Particles (VLPs) of FgVch9 reduced its conidiation capacity, perithecia formation, and pathogenicity for wheat and maize several folds. These results demonstrate that FgV-ch9 is associated with hypovirulence of *F. graminearum* (Darissa *et al.*, 2012).

Hypovirulence against *Rosellinia necatrix* (white root rot) :

Rosellinia necatrix, is a serious soilborne pathogen causes white root rot disease of fruit trees and other woody plants. Yaegashi *et al.* (2012) report forty-two sub-isolates of *R. necatrix*, after 2-3 years of inoculation into the apple trees in an orchard and found that all sub-isolate were genetically identical to W563 or NW10. However, 22 of the sub-isolates contained novel dsRNAs. Out of these six novel dsRNAs were isolated: S1 was a new victorivirus; S2, S3, and S4 were new partitiviruses; and S5 and S6 were novel viruses that could not be assigned to any known mycovirus family. These isolated mycoviruses have reduced mycelial growth, change in morphology and reduced pathogenicity. *R. necatrix* isolate W370 contains 12 segments of double-stranded RNA (dsRNA) that is believed to less virulent than the parent strain *R. necatrix* RT 37-1. When these mycoviruses contain strain N370 was inoculated in apple seedlings before their planting the mortality of seedlings

ranges from 0 to 16.7 per cent and 50 to 100 per cent for seedlings inoculated with the dsRNA-free strains *i.e.*, RT 37-1 and hence, it proves that mycoviruses present in fungal mycelium cause the hypovirulence (Kanematsu *et al.*, 2004).

Hypovirulence against *Sclerotinia sclerotiorum* :

Several different mycoviruses (ssRNA, dsRNA, and ssDNA viruses) have been identified in *S.sclerotiorum*. Thus, the *S.sclerotiorum* mycovirus system provides the opportunity to explore interactions between different types of mycoviruses and *S. sclerotiorum*. SsDRV confers hypovirulence in the strain Ep-1PN (Li *et al.*, 2000). Using the *S.sclerotiorum*-SsDRV system, 150 genes were identified that were down regulated in the strain Ep-1PN (Li *et al.*, 2008). The genes down regulated by SsDRV represented a broad spectrum of biological functions. Subsequently, the *S.sclerotiorum* integrin like gene (SSITL), which was suppressed in the presence of SsDRV, was further investigated via forward and reverse genetics approaches (Zhu *et al.*, 2013). In addition, mixed infections by two or more related or unrelated viruses are common in this fungus. Recently identified an ssDNA virus (SsHADV-1) and are establishing a *S.sclerotiorum* SsHADV-1 interaction system. Investigation of different *S.sclerotiorum* mycovirus interaction systems might supply new insights or clues regarding virus-host and virus-virus interactions as well as control strategies for *Sclerotinia* disease.

Hypovirulence against *Botrytis Species* (Gray mold disease) :

Gray mold disease, which is caused by *Botrytis* spp., is one of the most widespread and destructive fungal diseases of crops and postharvest fruits. Similar to other plant-pathogenic fungi, various mycoviruses are prevalent in the *Botrytis* population are *Botrytis* virus F (BVF), *Botrytis* virus X (BVX), *Botrytis cinerea* mitovirus 1 (BcMV1), and *Botrytis porri* RNA virus 1 (BpRV1) (Castro *et al.*, 2003; Howitt *et al.*, 1995 and Llorens *et al.*, 2013). BVF belongs to Mycoflexivirus in the family Gammflexiviridae, whereas BVX belongs to Botrexvirus in the family Alphaflexiviridae (King *et al.*, 2012). A mitovirus (BcMV1) was originally isolated from a hypovirulent strain (CanBc-1) in China (Zhang *et al.*, 2010 and Zhang *et al.*, 2007). Recently, BcMV1 was found in 55 per cent of the Spanish *Botrytis cinerea* isolates that contained mycoviruses (Llorens *et al.*, 2013).

In *Botrytis porri*, which is a sister species of *B. cinerea*, a novel bipartite dsRNA virus (BpRV1) was isolated from a hypovirulent strain (GarlicBc-72) (Wu *et al.*, 2012). BpRV1 is significantly different from partitivirus and RnMBV1. Thus, BpRV1 was considered to be a novel type of dsRNA virus.

Killer Phenomenon/Killer yeast :

Killer yeast is the yeast, such as *Saccharomyces cerevisiae*, which is able to secrete toxic proteins which are lethal to receptive cells. This phenomenon was first observed by Louis Pasteur in 1877. Killer isolates secrete proteins that are toxic to sensitive cells of the same or closely related species. Earlier, it was thought that the killer system in yeast has been a genetic phenomenon. It is now believed that a dsRNA virus is closely integrated with the yeast cells. The killer system also exists in *Ustilago maydis*. The killer strain secretes; a protein toxin that is lethal to sensitive strains. There are potentially interesting applications of killer yeast in medicine, food industry, and in agriculture. Presently, there is a no. of drugs available the market such as Killer Yeast - Vitality and wellness, Azo Yeast Tablets and ProFase, which are effective against various human ailments like Yeast infection and a potentially life threatening intestinal bacterial overgrowth. *Dipodascus capitatus* and a *Candida* sp. strains of yeasts, isolated from fruit and soil of Amazon, Atlantic Rainforests and organic farms having the killer yeast activities against the phytopathogen *Moniliophthora perniciosa* (syn. *Crinipellis perniciosa*) that causes the Witches broom disease of cocoa (Cabral *et al.*, 2009). Yeasts isolated from sugar cane and maize rhizosphere, leaves and stalks were screened for killer activities against *Colletotrichum sublineolum* and *Colletotrichum graminicola*, both causal agents of the anthracnose disease in sorghum and maize, respectively. Strains identified as *Torulasporea globosa* and *Candida intermedia* were able to inhibit the pathogen growth and having killer activity (Magri *et al.*, 2011). *Ustilago maydis*, a causal agent of corn smut disease, exhibit a 'killer' phenotype that is due to persistent infection by double-stranded RNA Totiviruses. These viruses produce potent killer proteins that are secreted by the host and kill competing, uninfected strains of *U. maydis*. *U. maydis* strains P4 and P6 that secrete killer proteins KP4 and KP6, respectively. When, KP4 is incorporated and expressed in maize, the resulting transgenic lines are immune to *U. maydis* infection (Allen *et al.*, 2013). Killer

phenomenon can be successfully used in the control of plant pathogenic fungi.

Increase in thermal tolerance of fungal host plant :

Fungi which are infected with dsRNA viruses have increased ability of the survival of the fungal host plant; when they are facing the high temperature regimes. Marquez *et al.* (2007), reported that the thermal tolerance of fungal host plant is a three way symbiosis i.e. interaction between virus, fungus and plant. Tropical panic grass inoculated with fungus containing *Curvularia thermal tolerance virus* (CThTV) is survived at temperature regime of 55 °C. When grown separately, neither the fungus nor the plant alone is able to grow at temperatures above 38°C, but symbiotically, they are able to tolerate elevated temperature regimes.

Mycovirus research in India :

In India, there is very less work done in the field of mycovirus and very less information available. Maheshwari and Gupta (1973), reported antiviral agents from *Aspergillus flavus*. Morphology, transmission and ultrastructure of VLP's in *Helminthosporium* spp. was described by Misra *et al.* (1979). Hexagonal VLP's 45 nm in diameter was detected in Himachal strain of *Trichothecium roseum* (George *et al.*, 1981). Tewari and Singh 1984 and 1985 isolated isometric VLP's from *Agaricus bisporus*. Later, Gupta (1990) conducted detailed studies on viruses of *R. solani* were purified and characterized.

Conclusion :

Majority of mycoviruses have segmented dsRNA in their genome and belong to family Hypoviridae, Totiviridae, Partitiviridae, Chrysoviridae and Reoviridae, that are found to infect fungi in phylum Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota. Various techniques are used for detection of these mycoviruses are direct electron-microscopic (EM), immunosorbent electron microscopy (IEM or ISEM), polyacrylamide gel electrophoresis (PAGE), enzyme-linked immunosorbent assay (ELISA) and reverse transcription polymerase chain reaction assay (RT-PCR). Mycoviruses can alter the phenotypes of infecting fungi such as reduced growth, pigmentation and lack of sporulation. Mycoviruses causes economical losses to mushroom industries. Mycoviruses can be used as biological control agents, because of the hypovirulence and killer phenomenon. Further structural and functional studies may help identify

the target proteins and those aspects of the antifungal proteins involved in specificity. In turn, this information may allow for the creation of antifungal proteins with a wider spectrum of activity and broader application in crops. Mycoviruses can be used for curing of various human diseases. Mycoviruses increase the thermal tolerance of fungal host plant. In future, we need to establish a system to explore hypovirulence-associated mycoviruses to control crop fungal diseases. Genetically modifying fungal strains must be developed to break the limitation of virus transmission that is caused by the host vegetative-incompatibility reaction, understanding the ecological properties of virus infected fungal strains and the mechanisms of virus transmission in fields, understanding the proper time for delivering mycovirus-infected strains in fields, and producing and formulating virus-infected fungal strains or virus particles for commercial use. At present, because of the lack of appropriate disease control strategies, control of plant pathogenic fungi is a difficult task. Use of fungicides possess health hazards and the risks to the environment, this is often cost prohibitive. Mycoviruses have the potential to control fungal diseases of crops when associated with hypovirulence. Continued advances in scientific technology, research on mycoviruses and their fungal hosts will provide new insights into the largely unknown world of mycoviruses.

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