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MINI REVIEW

Viruses of plant-pathogenic fungi: a promising biocontrol strategy for *Sclerotinia sclerotiorum*

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Abstract

Plant pathogenic fungi pose a significant and ongoing threat to agriculture and food security, causing economic losses and significantly reducing crop yields. Effectively managing these fungal diseases is crucial for sustaining agricultural productivity, and in this context, mycoviruses have emerged as a promising biocontrol option. These viruses alter the physiology of their fungal hosts and their interactions with the host plants. This review encompasses the extensive diversity of reported mycoviruses, including their taxonomic classification and range of fungal hosts. We highlight representative examples of mycoviruses that affect economically significant plant-pathogenic fungi and their distinctive characteristics, with a particular emphasis on mycoviruses impacting *Sclerotinia sclerotiorum*. These mycoviruses exhibit significant potential for biocontrol, supported by their specificity, efficacy, and environmental safety. This positions mycoviruses as valuable tools in crop protection against diseases caused by this pathogen, maintaining their study and application as promising research areas in agricultural biotechnology. The remarkable diversity of mycoviruses, coupled with their ability to infect a broad range of plant-pathogenic fungi, inspires optimism, and suggests that these viruses have the potential to serve as an effective management strategy against major fungi-causing plant diseases worldwide.

Keywords Mycovirus · Plant pathogenic fungi · Biocontrol · Hypovirulence · *Sclerotinia sclerotiorum*

Introduction

The Food and Agriculture Organization of the United Nations (FAO) defines food security as the continuous availability and access to nutritionally adequate and safe food to sustain an active and healthy life (Salinas et al. 2022; FAO 2023). With a growing global population, modern agriculture confronts numerous challenges in maintaining a steady supply of safe and high-quality food. These challenges encompass high fertilizer costs, climate change-associated impacts, and the emergence of pests and diseases (Meena et al. 2020; van Dijk et al. 2021). Pests and diseases typically result in average losses ranging from 20 to 40% of global agricultural productivity (Savary et al. 2019). In this context, similar to all living organisms, plants can suffer from infectious diseases that decrease their production. Plant pathogens, including protozoa, fungi, oomycetes, bacteria, phytoplasmas, viruses, viroids, and nematodes, lead to significant losses and damage in crops worldwide, substantially diminishing both the quality and quantity of agricultural products. These losses annually pose a significant threat to global food production (Savary et al. 2019).

Plant pathogenic fungi stand as one of the primary causes of plant diseases, posing a challenge to agriculture and food security. Controlling these diseases is pivotal in averting economic losses and ensuring food supply. Nevertheless, contemporary strategies for disease control must align with the concept of sustainable agriculture, which aims to produce pathogens free plants while minimizing the environmental impact of agricultural activities (Pingali 2012; Ramankutty et al. 2018). Chemical control has been extensively used in the management of plant diseases caused by fungi; nevertheless, fungicide resistance of fungi is steadily increasing on a global scale (Elderfield et al. 2018). Furthermore, the application of fungicides generates undesirable residues and can eliminate beneficial fungi due to their

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broad-spectrum action (van den Berg et al. 2013). Therefore, biocontrol strategies emerge as a sustainable option to be integrated into the management of fungal diseases. These strategies encompass the use of microorganisms (fungi and bacteria) or their bioactive secondary metabolites for biocontrol (Liu et al. 2020; Dimkić et al. 2022), the application of plant essential extracts (Raveau et al. 2020), biofumigation by incorporating fresh organic matter into the soil (Abdallah et al. 2020), and the induction of hypovirulence through mycoviruses (García-Pedrajas et al. 2019).

Mycoviruses are defined as viruses that infect fungi, and they have been described in all major groups of plant-pathogenic fungi for over 70 years (Hollings 1962; Pearson et al. 2009; Ghabrial and Suzuki 2009; Ghabrial et al. 2015). These viruses lack an extracellular infection route and are exclusively transmitted intracellularly through processes such as cell division, sporogenesis, and cell fusion. The only exception is Sclerotinia sclerotiorum hypovirulence-associated DNA virus 1 (SsHADV-1), which can be transmitted extracellularly to its host *Sclerotinia sclerotiorum*. Furthermore, their specificity is limited to individuals within the same vegetative compatibility group or closely related groups (Ghabrial et al. 2015; Lemus-Minor et al. 2019). Most known mycoviruses on plant-pathogenic fungi have positive-sense single-stranded RNA (+)ssRNA, and they were previously considered cryptic until the impact they can have on their fungal host by inducing hypovirulence (Pearson et al. 2009; Hough et al. 2023). Mycovirus-mediated hypovirulence is a phenomenon in which the ability of plant-pathogenic fungi to cause diseases is diminished as a result of viral infection (Nuss 2010). In this way, mycoviruses have emerged as promising biological entities with the potential to control the impact of fungal diseases in plants (Xie and Jiang 2014; Kotta-Loizou and Coutts 2017; Jia et al. 2021; Hough et al. 2023). These viruses alter the normal physiology of fungi, in addition to modifying their interactions with host plants, making them potential agents for disease control (Márquez et al. 2007; Zhou et al. 2021). Among the most studied plant-pathogenic fungi in the field of mycoviruses are *Botrytis cinerea*, *Fusarium* spp., *Magnaporthe oryzae*, *Puccinia striiformis*, *Rhizoctonia solani* and *Sclerotinia sclerotiorum*, with the latter being highlighted as the most extensively researched to date. The fungus *S. sclerotiorum* is a highly damaging necrotrophic pathogen that impacts over 500 plant species with considerable economic significance (Boland and Hall 1994; Hegedus and Rimmer 2005; Bolton et al. 2006). Its main effect is the induction of the disease commonly referred to as white mold, leading to stem rot in crops cultivated in diverse climatic conditions.

The main mycovirus families reported by the International Committee on Taxonomy of Viruses (ICTV) include single-stranded positive-sense RNA genomes such as *Botourmiaviridae*, *Fusariviridae*, *Mitoviridae*, *Hypoviridae*, and double-stranded RNA genomes *Chrysoviridae*. Over 250 mycoviruses have been reported in various studies for *S. sclerotiorum*, emphasizing Sclerotinia sclerotiorum mycoreovirus 4 (SsMYR4), Sclerotinia sclerotiorum hypovirulence-associated DNA virus 1 (SsHADV-1), Sclerotinia sclerotiorum debilitation-associated RNA virus (SsDRV), and Sclerotinia sclerotiorum partitivirus 1 (SsPV1) (Xie et al. 2006; Yu et al. 2010; Xie and Jiang 2014; Wu et al. 2017).

This review aims to establish the state of the art regarding the use of mycoviruses infecting plant-pathogenic fungi as a biocontrol strategy. It addresses the distinctive characteristics and diversity of these viral particles and their mechanisms of action, transmission, and ecology. Furthermore, it discusses the challenges for their implementation, information gaps, and the necessary focus for future research, with the goal of making this biocontrol alternative a feasible strategy to be integrated into the management of fungal pathogens as part of an integrated approach.

Early studies on mycoviruses

The origin of mycoviruses remains elusive, although two main hypotheses are proposed: ancient coevolution over millions of years with their host infections or the recent adaptation of these viruses, which initially infected plants and shifted to fungi as hosts (Pearson et al. 2009). While mycoviruses share certain characteristics with viruses that infect animals and plants, they are distinguished by their lack of an extracellular infection route and a movement protein found in animal and plant viruses (Howitt et al. 2001; Ghabrial et al. 2015). The earliest indications of the existence of mycoviruses emerged from research involving extracts obtained from liquid cultures of *Penicillium funiculosum* and *P. stoloniferum*, microscopic fungi belonging to the class Ascomycetes (Powell et al. 1952; Shope 1953). Nevertheless, the first formal report of a mycovirus dates to the 1960s when at least three types of viruses were identified in diseased specimens of *Agaricus bisporus*, which exhibited deformed fruiting bodies and reduced growth (Hollings 1962). This event marked the beginning of a fascinating tale of discovery and scientific exploration known as modern mycovirology (Ghabrial et al. 2015).

Mycovirology is defined as the field dedicated to the study of mycoviruses, focusing on their taxonomy, host range, origin, evolution, transmission, and movement. However, the ability of mycoviruses to induce hypovirulence in plant-pathogenic fungi is their main focus of study as a potential biocontrol method (Nuss 2005). Hypovirulence caused by mycoviruses was first described by Grente (1965), who observed a reduction in the growth of *Cryphonectria parasitica*, accompanied by a decrease in spore formation and interference with sexual reproduction, as a result of infection with the mycovirus CHV-1. Following this report, it was elucidated that these mycoviruses were responsible for several instances of "spontaneous cure" that had been documented in various crops in previous years (Grente and Berthelay-Sauret 1978) and attenuated strains of these fungi containing mycoviruses began to be identified and isolated. The National Institute for Agricultural Research (INRA) of France can be considered a pioneer in biological control using mycoviruses. From 1966 to 1974, they conducted tests on the application of mycoviruses in 500 hectares of chestnut (*Castanea sativa*) plantations. They reported a 70% cure rate of inoculated cankers after five years of application. The success was significant, leading to funding from the Ministry of Agriculture, allowing them to implement the method in 18,000 hectares across France between 1974 and 1978 (Grente and Berthelay-Sauret 1978). These advancements laid the foundation for the use of mycoviruses as effective tools for controlling fungal diseases in agriculture.

Understanding mycovirus mechanisms

Mycoviruses employ distinctive transmission mechanisms that enable them to propagate within fungal populations, including plant-pathogenic fungi. Unlike many viruses in animals and plants, most mycoviruses lack extracellular infection routes and natural vectors, relying instead on intracellular transmission pathways (Buck 1998). One prominent mechanism is horizontal transmission through hyphal anastomosis, where hyphae from different fungal individuals fuse, allowing the transfer of mycoviruses (Xie et al. 2006). Vertical transmission occurs during sporogenesis when mycoviruses are passed from mother to their offspring through spores (Buck 1998), with the exception of Sclerotinia sclerotiorum hypovirulence-associated DNA virus 1, which can infect the fungus extracellularly (Yu et al. 2013). These forms of transmission promote the expansion of mycoviruses within fungal populations and contribute to their persistence.

Mycoviruses exert their effects on fungal hosts through a wide variety of mechanisms. The first is of a "cryptic nature," where many mycoviruses establish latent infections, and no apparent changes in the morphology of the fungus are observed (Hyder et al. 2013; Ghabrial et al. 2015; Son et al. 2015). Other mycoviruses induce changes in fungal physiology, resulting in altered growth patterns, abnormal pigmentation, and modified sexual reproduction. This phenomenon is known as "hypovirulence," presenting as a reduction in the virulence of the fungal host and providing a potential biocontrol mechanism against diseases in plants (van Diepeningen et al. 2008; Lee et al. 2011; García-Pedrajas et al. 2019). Hypovirulence can be attributed to factors such as the expression of proteins encoded by the virus that interfere with the fungal virulence factors or activate host defense responses (Castro et al. 2003; Lemus-Minor et al. 2019; Sukphopetch et al. 2021). Furthermore, mycoviruses can alter gene expression or disrupt cellular processes to modulate the interaction between the fungus and its environment (Kotta-Loizou 2021; Applen Clancey et al. 2020). On the other hand, some studies have reported that certain mycoviruses can enhance the virulence of the host fungus, a phenomenon referred to as "hypervirulence." This effect may not be desirable in mycovirus–fungus interactions, but it can exhibit characteristics that are beneficial in the virus–fungus–plant interaction (Kotta-Loizou et al. 2015; Shah et al. 2020; Kotta-Loizou 2021).

As mentioned earlier, some mycoviruses remain in a latent state, while others produce symptoms (Pearson et al. 2009; Son et al. 2015). There are several causes and mechanisms that can explain why mycoviruses induce different responses in fungi. Some mycoviruses modulate the expression of genes that often encode proteins that interfere with metabolic pathways; for example, they can inhibit the production of enzymes necessary for fungal pathogenicity (Allen et al. 2003). As a result, the fungus becomes less virulent and less capable of causing diseases in host plants, although the nature of these metabolic pathways is still mostly unknown (Kotta-Loizou 2021). Mycoviruses can directly interfere with the replication and growth of the fungus, affecting its DNA, RNA, or protein synthesis, which reduces its ability to multiply and, therefore, its capacity to infect and damage plants (Chen et al. 1994; Kotta-Loizou 2021). They can also induce changes in the morphology and physiology of the fungus (Li et al. 2008; Ko et al. 2021); for instance, they can alter spore production and release or modify the production of cellular structures. These changes can weaken the fungus's ability to colonize and damage the host plant (Shi et al. 2019). Furthermore, they can compete with other viruses or genetic elements present in the fungus and this competition can reduce the ability of other pathogens to cause plant diseases (Ahn and Lee 2001; Márquez et al. 2007).

The dynamic interaction between mycoviruses and their fungal hosts is determined by a complex interplay of factors. Mycoviruses can establish both persistent and transient infections within fungal populations. Persistent infections occur when mycoviruses infect a fungal host persistently without causing visible symptoms. In contrast, transient infections result in visible symptoms such as changes in mycelial growth or alterations in reproductive structures (Nuss 2010). The outcome of mycovirus-host interactions depends on the specific combination of mycovirus and fungus, the physiological state of the host, and environmental conditions. Variables such as temperature, nutrient availability, and stress factors can influence the outcome of these interactions (Kotta-Loizou 2021). In some cases, the presence of mycoviruses can confer an adaptive advantage to the host, leading to the coexistence of mycoviruses and their fungal hosts over extended periods (Myers and James 2022).

Understanding the mechanisms of mycovirus transmission, their modes of action, and the dynamics of mycovirus–host interactions paves the way for their application in plant disease management. Exploiting mycoviruses as biocontrol agents holds significant promise, as they can potentially modulate the virulence of plant-pathogenic fungi and reduce the impact of plants diseases. Furthermore, unraveling the interactions between mycoviruses and their fungal hosts provides valuable insights into the coevolutionary dynamics between viruses and fungi, helping us gain a deeper understanding of the fascinating world of fungal–viral interactions.

Diversity of mycoviruses in plant-pathogenic fungi

Mycoviruses exhibit remarkable diversity concerning their genomic structure, replication strategies, and evolutionary relationships (Kondo et al. 2022). The genomic composition of mycoviruses that infect plant-pathogenic fungi mainly comprise positive-sense single-stranded RNA (58.2%) or double-stranded RNA (30.8%). Nonetheless, mycoviruses with single-stranded circular DNA genomes (±) ssDNA and negative-sense single-stranded (−) ssRNA mycoviruses have also been identified (Ghabrial et al. 2015; ICTV 2023; Hough et al. 2023). Regarding mycoviruses from major fungal pathogens, there are at least 237 mycoviruses reported in the (ICTV), classified into 22 families, and one unclassified mycovirus (Botrytis porri botybirnavirus 1). Among the primary families of mycoviruses from plant-pathogenic fungi are *Botourmiaviridae* (12.1%) and *Fusariviridae* (11.0%) with (+) ssRNA genomes, as illustrated in Fig. 1. Recent advances in sequencing technologies and metagenomic approaches have significantly contributed to the identification of an expanding repertoire of new mycoviruses, enriching our understanding of their genetic composition and classification (Mu et al 2021a, b; Jia et al 2021; Ruiz-Padilla et al. 2021; Wang et al. 2022; Luo et al 2022; Ye et al. 2023).

Potential of mycoviruses against major plant-pathogenic fungi

The potential of mycoviruses against major from plant-pathogenic fungi has been extensively studied, revealing promising prospects in the field of plant pathology. These viruses have been primarily detected in plant-pathogenic and endophytic fungal species within the Ascomycota division

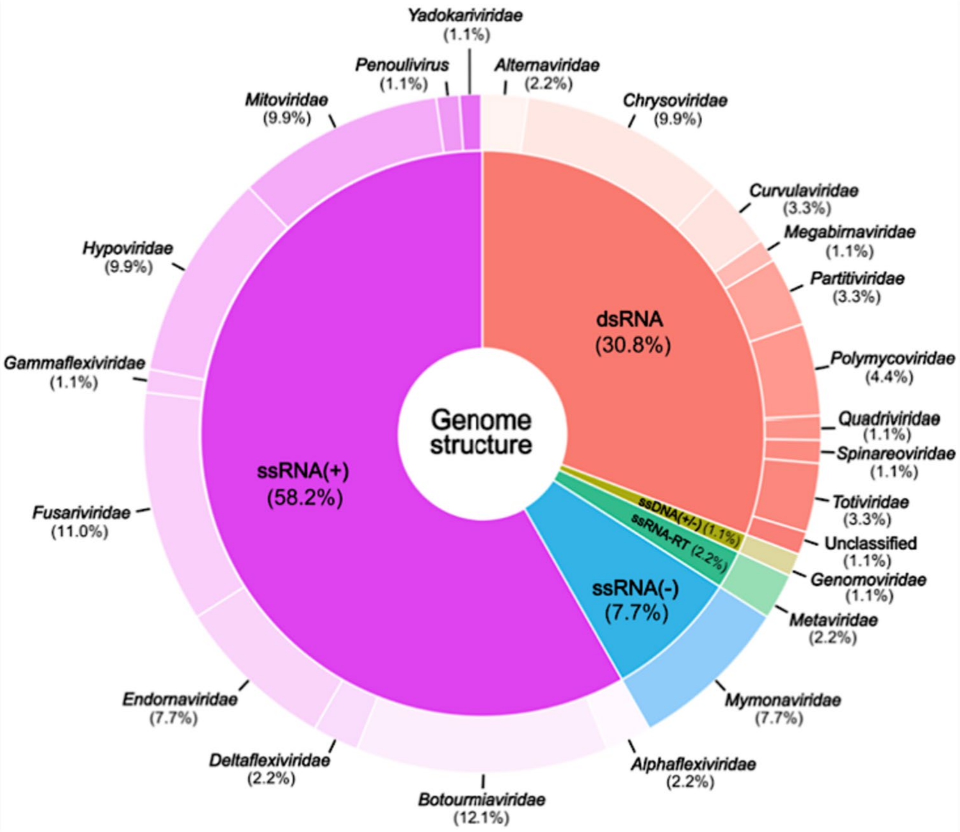

Fig. 1 Genomic structure of mycoviruses families affecting the main plant-pathogenic fungi

(Myers and James 2022). Among the plant-pathogenic fungi investigated for biocontrol using mycoviruses, *Botrytis cinerea* stands out as a devastating pathogen responsible for gray mold disease in various vegetable, fruit, and ornamental crops. It has the capacity to infect over 1400 plant species (Williamson et al. 2007; Dean et al. 2012). To date, at least 35 species of mycoviruses infecting this fungus have been documented (ICTV 2023). The first reports of these infections date back to the 1980s (Hiratsuka et al. 1987). Within the *Sclerotiniaceae* family, to which *Botrytis cinerea* and *Sclerotinia sclerotiorum* belong, various types of genomes have been identified, including (+) ssRNA, (−) ssRNA, ssDNA, and an unclassified mycovirus with a dsRNA genome (Fig. 2).

Recently, a study uncovered 92 mycoviruses in *Botrytis cinerea* isolates from grapes in Italy and Spain, expanding our knowledge in the field of mycovirology. It is worth noting that not all of these newly discovered mycoviruses have been officially accepted by the ICVT at this time. This discovery highlights the diversity and potential significance of mycoviruses in the context of plant pathogens and their management (Ruiz-Padilla et al. 2021). Several mycoviruses have been associated with the reduction of virulence in *Botrytis cinerea* isolates across different locations and hosts, suggesting the feasibility of using mycoviruses as a biocontrol strategy against this fungus. Examples include Botrytis cinerea mitovirus 1, Botrytis cinerea hypovirus 1, and Botrytis cinerea partitivirus 2. These mycoviruses show promise in attenuating the virulence of *Botrytis cinerea* and can potentially be harnessed as biocontrol agents to protect crops from gray mold disease (Wu et al. 2010; Hao et al. 2018; Kamaruzzaman et al. 2019). Furthermore, research suggests the potential of mycoviruses to induce hypovirulence as a biocontrol strategy against diseases caused by *B. cinerea*. However, other studies indicate that their effectiveness may be limited by environmental conditions and competition with other microorganisms (Guetsky et al. 2001; Gielen et al. 2004).

Another significant pathogen is *Fusarium*, responsible for causing severe damage to most agricultural and forest crops (Sharma et al. 2018). Many mycoviruses that infect *Fusarium* species remain in a latent state, but some have demonstrated hypovirulence, including Fusarium graminearum virus 1 (FgV1), Fusarium graminearum virus-ch9 (FgV-ch9), Fusarium graminearum hypovirus 2 (FgHV2), and Fusarium oxysporum f. sp. dianthi mycovirus 1 (FodV1). These mycoviruses have the potential to reduce the virulence of Fusarium species and could be explored as biocontrol agents to mitigate the damage caused by these pathogens (Paudel et al. 2022).

Magnaporthe oryzae, the causal agent of rice blast disease represents one of the major constraints to worldwide rice production. Within this pathogen, several mycoviruses have been identified, including Magnaporthe oryzae virus 1 (MoV1), Magnaporthe oryzae chrysovirus 1 (MoCV1), Magnaporthe oryzae chrysovirus 2 (MoCV2), Magnaporthe oryzae partitivirus 1 (MoPV1), Magnaporthe oryzae partitivirus 2 (MoPV2), and Magnaporthe oryzae botybirnavirus 1 (MoBV1). These mycoviruses have the potential to reduce the virulence of *M. oryzae*, offering possible approaches for disease control strategies aimed at mitigating the impact of rice blast disease on rice production (Moriyama et al. 2018; Owashi et al. 2020).

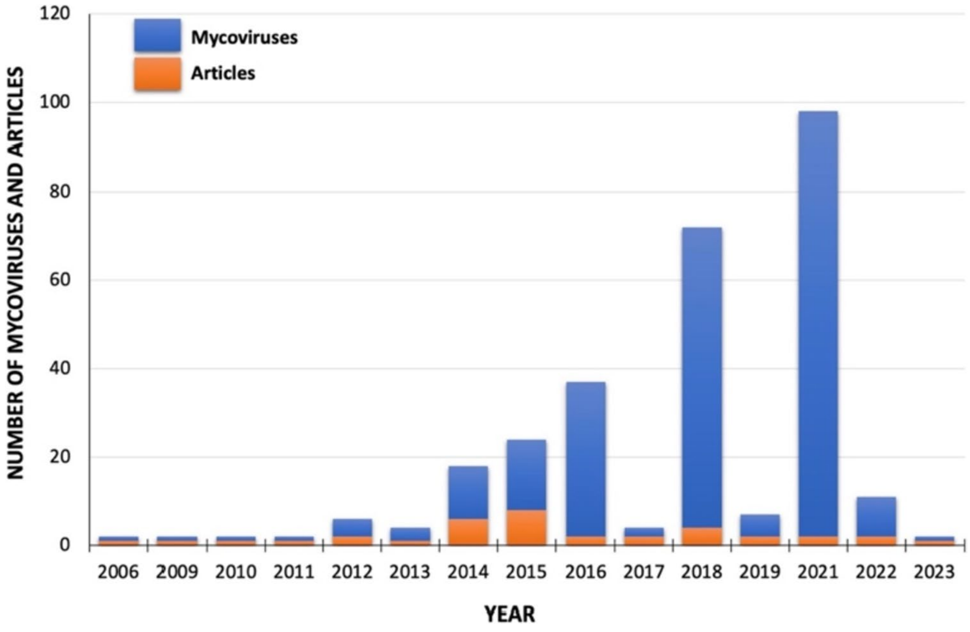

Fig. 2 Number of publications on mycovirus species associated with *Sclerotinia sclerotiorum* per year of publication

Regarding *Puccinia striiformis*, another significant fungus that causes stripe rust disease in wheat and other cereals, research has revealed the presence of several mycoviruses (Zheng et al. 2017), including Puccinia striiformis mitovirus 1 (PsMV1). This mycovirus has been shown to hinder the growth and sporulation of *P. striiformis*, offering promise for strategies aimed at managing this fungus (Zheng et al. 2019).

Rhizoctonia solani, a soil-borne pathogen, causes root rot and damping-off diseases in various crops. In this pathogen, more than 100 viruses with dsRNA, (+) ssRNA and (−) ssRNA genomes, as well as unclassified RNA elements, have been identified (Abdoulaye et al. 2019). As an example, the mycovirus Rhizoctonia solani partitivirus 2 (RsPV2) is characterized by its segmented double-stranded RNA genome. This virus has the potential to influence the growth and pathogenicity of *R. solani*, representing an opportunity for inclusion in disease management approaches (Li et al. 2022).

The exploration of these mycoviruses and their interactions with key plant-pathogenic fungi offer a promising avenue for the development of effective disease control strategies. By unraveling the mechanisms underlying these interactions, we can harness the potential of mycoviruses to combat devastating fungal diseases and sustain agricultural productivity.

Case of *Sclerotinia sclerotiorum*

The fungus *Sclerotinia sclerotiorum* is indeed a highly destructive necrotrophic pathogen that affects over 500 plant species of significant economic importance. It can infect a wide range of plant families, including *Brassicaceae*, *Fabaceae*, *Solanaceae*, *Asteraceae*, *Apiaceae,* and *Malvaceae*, as well as various ornamental plants (Boland and Hall 1994; Hegedus and Rimmer 2005; Bolton et al. 2006). This fungus primarily causes the disease known as white mold, resulting in stem rot in crops grown under various climatic conditions, including temperate zones, tropical regions, and arid areas. This leads to significant yield losses, as documented in several studies (Mehta 2009; Lehner et al. 2017; Hossain et al. 2023), and it can cause the death of plants within a very short period, often less than a week from the onset of infection. Furthermore, this pathogen can accumulate in the edible parts of plants, posing a negative factor for their marketability. Given its ability to infect a wide range of plants and thrive in diverse climatic conditions, *Sclerotinia sclerotiorum* presents a significant challenge to agriculture and food security. For this reason, various management strategies, including the use of mycoviruses and other biological control alternatives, are being investigated to reduce the impact of this pathogen (Dilantha et al. 2004).

Managing white mold disease is exceptionally challenging due to the absence of cultivars resistant to the pathogen. In addition, the fungus produces sclerotia, which are resistant structures that can persist in the soil for years until they encounter suitable conditions for germination, either by myceliogenic or carpogenic means, producing ascospores, which serve as a source of dispersion. Low temperatures and excess humidity are factors that facilitate the growth of pathogen, and these characteristics make it difficult to control *S. sclerotiorum* (Dilantha et al. 2004; Faruk and Rahman 2022). Therefore, effective management strategies are needed to mitigate the economic and environmental impact of the disease. In recent years, mycoviruses have emerged as a promising biocontrol method for *S. sclerotiorum*. These viruses can infect the fungal host and cause a reduction in virulence, altered growth, and even the complete loss of the ability to cause disease (Jia et al. 2021; Kotta-Loizou et al. 2021; Mu et al. 2021b).

Isolates of *S. sclerotiorum* are infected by a wide diversity of mycoviruses (Marzano et al. 2016; Mu et al. 2018; Mu et al. 2021a, b), and in recent years, there has been an increasing number of reports of mycovirus species due to advances in genomic sequencing techniques and improvements in bioinformatics tools, as shown in Fig. 3.

The ICTV lists 477 mycoviruses, including 237 mycoviruses from plant-pathogenic fungi, with 29 mycoviruses known to affect *S. sclerotiorum*. However, in this review, there are various publications reporting more than 230 mycoviruses that can infect this pathogen; China, USA, and New Zealand are at the forefront of mycovirus research worldwide, where 30 different families of mycoviruses have been reported (Fig. 4).

Some examples of mycoviruses that induce hypovirulence in *S. sclerotiorum* include: Sclerotinia sclerotiorum hypovirulence-associated DNA virus 1 (SsHADV-1), Sclerotinia sclerotiorum debilitation-associated RNA virus (SsDRV/Ep-1PN), Sclerotinia sclerotiorum RNA virus L (SsRV-L), Sclerotinia sclerotiorum hypovirus 1 (SsHV1/SZ-150), and Sclerotinia sclerotiorum mitovirus 1 and 2 (SsMV1 and SsMV2) (Xie et al. 2006; Yu et al. 2010; Xie et al. 2011; Xie and Ghabrial 2012). Among the mycoviruses that have shown better results in hypovirulence assays are Sclerotinia sclerotiorum partivirus 1 (SsPV1), which causes reduced virulence in soybean leaves and exhibits typical hypovirulence characteristics in the host (Xiao et al. 2014). Sclerotinia sclerotiorum botybirnavirus 1 (SsBRV1) in the SCH941 isolate did not induce lesions in rapeseed leaves (Liu et al. 2015). Other viruses, such as Sclerotinia sclerotiorum mitovirus 1 (SsMV1), Sclerotinia sclerotiorum narnavirus 4 (SsNV4), Sclerotinia sclerotiorum ourmia-like virus 14 (SsOLV14), Sclerotinia sclerotiorum ourmia-like virus 22 (SsOLV22), and Sclerotinia sclerotiorum negative-stranded RNA virus 1 (SsNsRV-1),

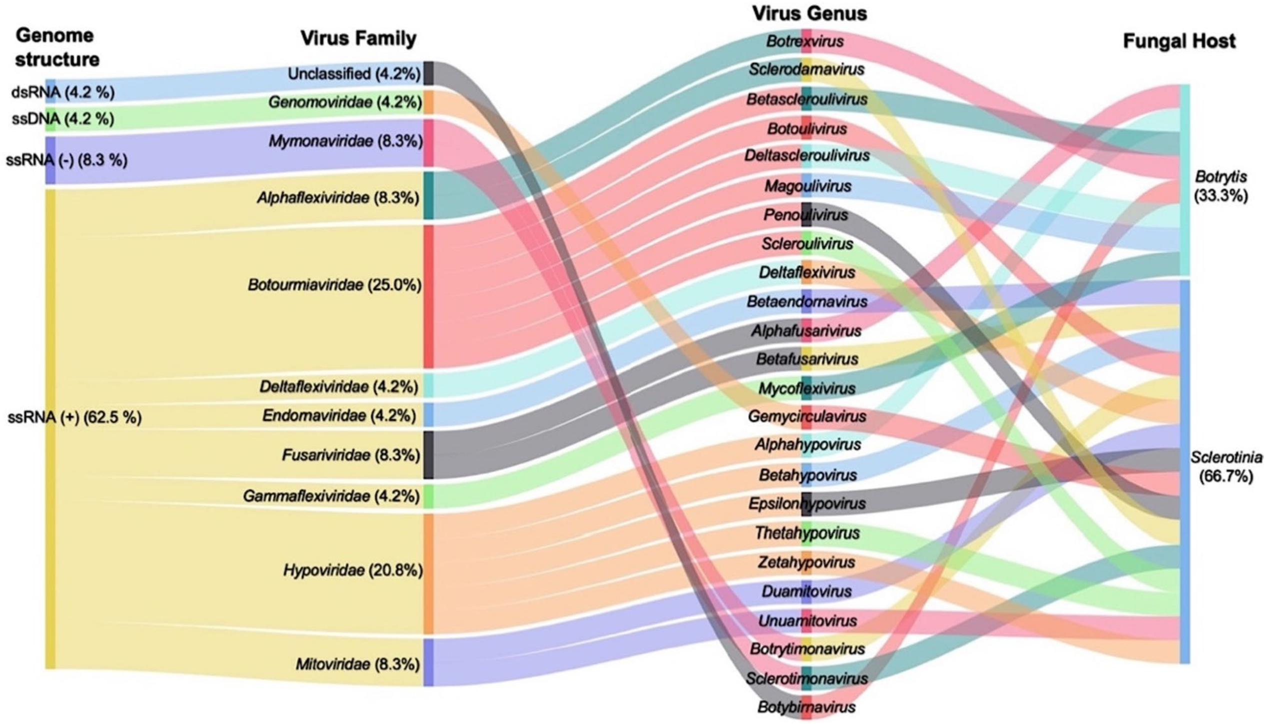

Fig. 3 Genome structure and taxonomy of mycoviruses infecting fungi within the *Sclerotinaceae* family, based on data reported in ICTV

caused a hypovirulent effect in the HC025 and SCH941 isolates of *S. sclerotiorum* (Liu et al. 2015; Wang et al. 2022). A hypovirulent isolate (228) of *S. sclerotiorum*, did not produce typical lesions in rapeseed leaves. It was demonstrated that Sclerotinia sclerotiorum deltaflexivirus 2 (SsDFV2) could be efficiently transmitted to vegetatively incompatible individuals through dual culture (Hamid et al. 2018). More detailed information about the mycoviruses reported so far that cause hypovirulent effects in *S. sclerotiorum* is described in Table 1.

Several studies have demonstrated the efficacy of mycoviruses as a method for biological control of *S. sclerotiorum*. For example, Sclerotinia sclerotiorum hypovirulence-associated DNA virus 1 (SsHADV-1) has been shown to significantly reduce the virulence of *S. sclerotiorum* in various crops, including soybean (*Glycine max*), canola (*Brassica napus*), and lettuce (*Lactuca sativa*) (Yu et al. 2010). Research has shown particular interest in Sclerotinia sclerotiorum mycoreovirus 4 (SsMYRV4) and Sclerotinia sclerotiorum partitivirus 1 (SsPV1) because they overcome vegetative incompatibility by altering genes in the host fungus, which naturally occurs when two hyphae or mycelia from two different fungal isolates cannot fuse or grow together. This is due to the presence of recognition and signaling systems (vic loci) that prevent hyphae from different strains from merging and sharing their cytoplasmic contents (Xie and Jiang 2014; Zhang and Nuss 2016; Wu et al. 2017; Khan et al. 2023a).

However, there are still some limitations in the current understanding of RNA mycoviruses as a biocontrol method for *S. sclerotiorum*, as the specific mechanisms by which RNA mycoviruses exert their effects are not yet fully understood (García-Pedrajas et al. 2019).

Challenges in the application of mycoviruses

While mycoviruses hold promise for various applications, there are also certain challenges to consider, which are listed below.

Limited host range

Mycoviruses often have a narrow host range, meaning they can only infect specific fungal species or isolates (van Diepeningen 2021). This limits their potential applicability as broad-spectrum biocontrol agents for plant pathogens. Therefore, each mycovirus–fungus interaction must be carefully evaluated, and the efficacy of a mycovirus can vary among different fungal pathogens.

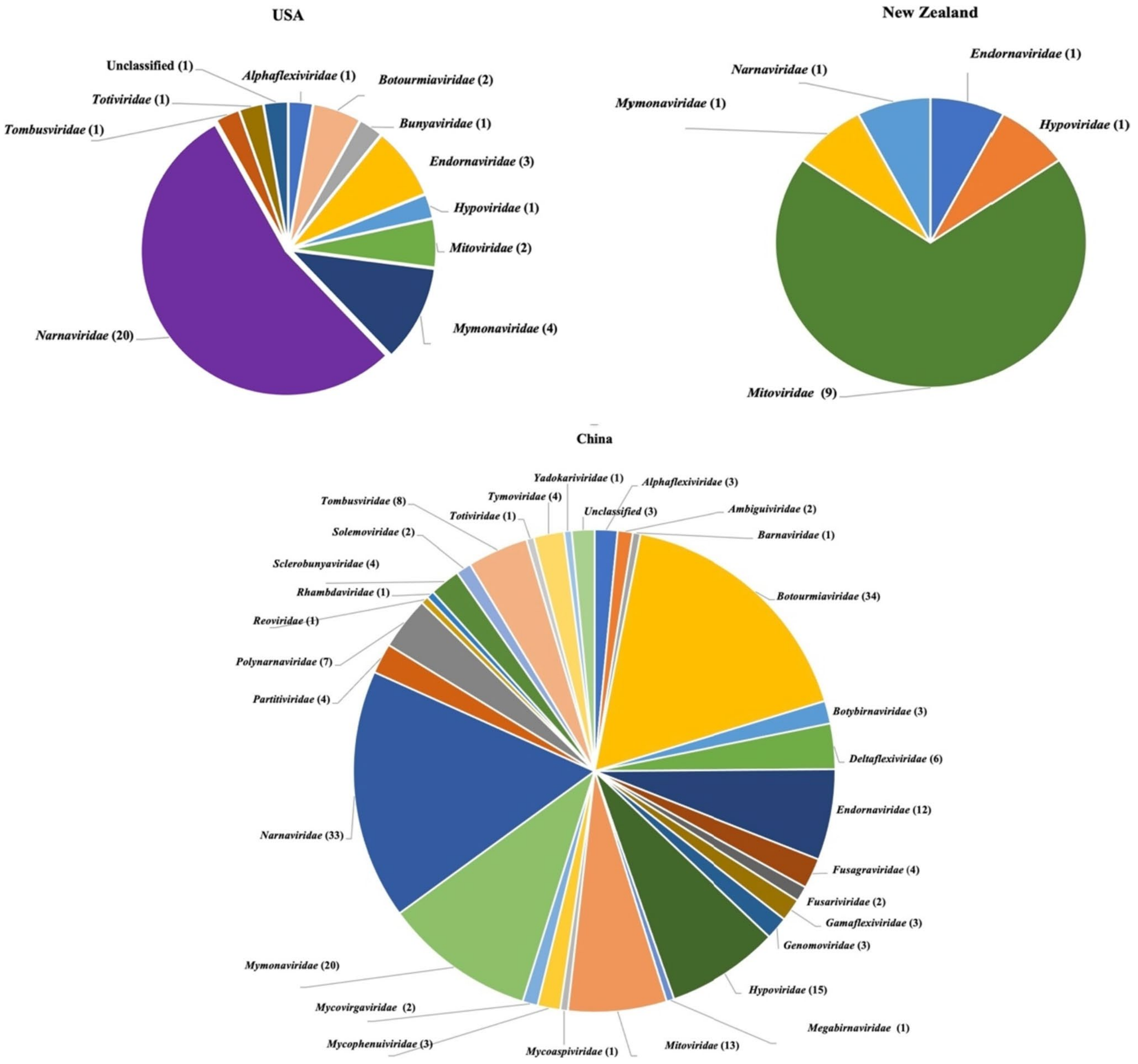

Fig. 4 Families of mycoviruses and the number of reported species infecting *Sclerotinia sclerotiorum* by country

Instability and loss of disease attenuation

Mycoviruses can undergo genetic changes and evolve within the fungal host leading the loss of desired characteristics, such as virulence reduction or disease attenuation (Hough et al. 2023). Precisely, these changes can result from viral mutations or recombination events, making the long-term stability of disease control mediated by mycoviruses uncertain.

Unpredictable interactions

The interactions between mycoviruses and their fungal hosts can be complex and not fully understood. Mycoviruses can have both positive and negative effects on their hosts, ranging from reduced virulence to altered growth and other physiological changes (Chiba et al. 2013; Khan et al. 2023a). Unintended consequences may arise when introducing mycoviruses into field environments, including the

Table 1 Mycovirus species reported with hypovirulent effect in *Sclerotinia sclerotiorum*

Genome	Mycoviruses	Mycoviruses name	Family	Host	Reduction (%) in lesion diameter	Country	References
dsRNA	SsDV	Sclerotinia sclerotiorum dsRNA virus	Unclassified	Celery	65.88	USA	Boland 1992
dsRNA	SsMV2	Sclerotinia sclerotiorum mitovirus 2	*Narnaviridae*	Tomato	66.66 (combined)	New Zealand	Khalifa and Pearson 2013
dsRNA	SsMV3	Sclerotinia sclerotiorum mitovirus 3	*Narnaviridae*				
dsRNA	SsMV4	Sclerotinia sclerotiorum mitovirus 4	*Narnaviridae*				
dsRNA	SsPV1	Sclerotinia sclerotiorum partivirus 1	*Partitiviridae*	Soybean	94.44	China	Xiao et al. 2014
dsRNA	SsBRV1	Sclerotinia sclerotiorum botybirnavirus 1	*Botybirnaviridae*	Rapeseed	100	China	Liu et al. 2015
dsRNA	SsMV1	Sclerotinia sclerotiorum mitovirus 1	*Narnaviridae*	Rapeseed	70.83	China	Xu et al. 2015
dsRNA	SsMBV1	Sclerotinia sclerotiorum megabirnavirus 1	*Megabirnaviridae*	Rapeseed	74.07	China	Wang et al. 2015
dsRNA	SsBRV2	Sclerotinia sclerotiorum botybirnavirus 2	*Botybirnaviridae*	Soybean	46.75	China	Ran et al. 2016
dsRNA	SsMYRV4	Sclerotinia sclerotiorum mycoreovirus 4	*Reoviridae*	Rapeseed	72.09	China	Wu et al. 2017
dsRNA	SsOV17	Sclerotinia sclerotiorum ourmiavirus 17	*Botourmiaviridae*	Rapeseed	No available	China	Mu et al. 2021a
dsRNA	SsMV1	Sclerotinia sclerotiorum mitovirus 1	*Narnaviridae*	Rapeseed	100 (combined)	China	Wang et al. 2022
dsRNA	SsNV4	Sclerotinia sclerotiorum narnavirus 4	*Narnaviridae*				
dsRNA	SsOLV14	Sclerotinia sclerotiorum ourmia-like virus 14	*Botourmiaviridae*				
dsRNA	SsOLV22	Sclerotinia sclerotiorum ourmia like virus 22	*Botourmiaviridae*				
(−) ssRNA	SsNsRV-1	Sclerotinia sclerotiorum negative-stranded RNA virus 1	*Mymonaviridae*				
(+) ssRNA	SsDRV	Sclerotinia sclerotiorum debilitation-associated RNA virus	*Alphaflexiviridae*	Rapeseed	No available	China	Xie et al. 2006
(+) ssRNA	SsRV-L	Sclerotinia sclerotiorum RNA virus L	*Alphaflexiviridae*	Eggplant	90.90	China	Liu et al. 2009

Table 1 (continued)

Genome	Mycoviruses	Mycoviruses name	Family	Host	Reduction (%) in lesion diameter	Country	References
(+) ssRNA	SsHV1	Sclerotinia sclerotiorum hypovirus 1	*Hypoviridae*	Rapeseed	100	China	Xie et al. 2011
(+) ssRNA	SsMV1	Sclerotinia sclerotiorum mitovirus 1	*Mitoviridae*	Soybean and lettuce	No available	USA	Xie and Ghabrial 2012
(+) ssRNA	SsMV2	Sclerotinia sclerotiorum Mitovirus 2	*Mitoviridae*				
(+) ssRNA	SsHV2	Sclerotinia sclerotiorum hypovirus 2	*Hypoviridae*	Tomato	60	New Zealand	Khalifa and Pearson 2014
(+) ssRNA	SsHV2	Sclerotinia Sclerotiorum hypovirus 2	*Hypoviridae*	Rapeseed	70.82	China	Hu et al. 2014
(+) ssRNA	SsHV2L	Sclerotinia sclerotiorum hypovirus 2 Lactuca	*Hypoviridae*	Soybean and lettuce	62.5	USA	Marzano et al. 2015
(+) ssRNA	SsDFV1	Sclerotinia sclerotiorum deltaflexivirus 1	*Deltaflexiviridae*	Rapeseed	No available	China	Li et al. 2016
(+) ssRNA	SsDFV2	Sclerotinia sclerotiorum deltaflexivirus 2	*Deltaflexiviridae*	Rapeseed	100	China	Hamid et al. 2018
(+) ssRNA	HuSRV1	Hubei sclerotinia RNA virus 1	*Solemoviridae*	Rapeseed	43.18	China	Azhar et al. 2019
(+) ssRNA	SsOLV4	Sclerotinia sclerotiorum ourmia-like virus 4	*Botybirnaviridae*	Rapeseed	51.11	China	Wang et al. 2020
dsRNA	SsBV3	Sclerotinia sclerotiorum botybirnavirus 3	*Botourmiaviridae*	Rapeseed	90.38 (combined)	China	Mu et al. 2021b
(+) ssRNA	SsEV3	Sclerotinia sclerotiorum endornavirus 3	*Endornaviridae*				
(+) ssRNA	SsHV1	Sclerotinia sclerotiorum hypovirus 1	*Hypoviridae*				
(+) ssRNA	SsMTV1	Sclerotinia sclerotiorum mycotimovirus 1	*Tymoviridae*				
(+) ssRNA	SsOV4	Sclerotinia sclerotiorum ourmia-like virus 4	*Botourmiaviridae*				
(+) ssRNA	SsDFV3	Sclerotinia sclerotiorum deltaflexivirus 3	*Deltaflexiviridae*				
(+) ssRNA	SsOV5	Sclerotinia sclerotiorum ourmia-like virus 5	*Botourmiaviridae*				

Table 1 (continued)

Genome	Mycoviruses	Mycoviruses name	Family	Host	Reduction (%) in lesion diameter	Country	References
(+) ssRNA	SsMAV1	Sclerotinia sclerotiorum mycoalphavirus virus 1	Unclassified				
(−) ssRNA	SsRhV1	Sclerotinia sclerotiorum rhambdovirus 1	*Rhabdoviridae*				
(+) ssRNA	SsEV11	Sclerotinia sclerotiorum endornavirus 11	*Endornaviridae*	Rapeseed	33.86	China	Luo et al. 2022
(+) ssRNA	SsAFV1	Sclerotinia sclerotiorum alphaflexivirus 1	*Alphaflexiviridae*	Rapeseed	22.44	USA	Ye et al. 2023
(−) ssRNA	SsNsRV-1	Sclerotinia sclerotiorum negative stranded RNA virus 1	*Mymonaviridae*	Rapeseed	100	China	Liu et al. 2014
ssDNA	SsHADV-1	Sclerotinia sclerotiorum hypovirulence associated-DNA virus 1/sclerotinia gemycircularvirus 1	*Genomoviridae*	Rapeseed	No data available	China	Yu et al. 2010

disruption of fungal biology or undesired effects on non-target organisms.

Limited availability and practical application

Mycoviruses that show promise for disease control may not be readily available or accessible for practical application. Isolating and characterizing specific mycoviruses can be time-consuming, and scaling up production for large-scale field use presents challenges (Khan et al. 2023b; Villan Larios et al. 2023). Furthermore, the practical implementation of mycoviruses as biocontrol agents requires careful evaluation, production methods, and consideration of regulatory aspects (van Diepeningen 2021; Khalifa et al. 2021).

Lack of complete control

Mycoviruses can reduce the severity of disease caused by plant-pathogenic fungi, but complete eradication or prevention of infections will not be achieved solely through mycovirus application. Therefore, the integration of mycoviruses with other disease management strategies, such as cultural practices, fungicides, or resistant crops, may be necessary for effective disease control (García-Pedrajas et al. 2019; O'Sullivan et al. 2021).

Indeed, it is important to consider that ongoing research and technological advancements aim to address some of these limitations. Researchers are working to enhance our understanding of mycovirus-host interactions, develop methods for stable and controlled applications, and explore novel approaches to manipulate mycoviruses to improve their efficacy and stability in field environments.

Considerations in the application of mycoviruses for plant disease management

To maximize the efficacy of mycoviruses, careful consideration should be given to the selection of specific mycoviruses (Fig. 5). It is crucial to identify and choose mycoviruses that exhibit desired characteristics for controlling plant pathogens. Factors to consider include the ability to attenuate pathogenicity, reduce disease symptoms, or enhance resistance in the host. Ideally, a mycovirus should have a high level of stability and compatibility with the target fungal pathogen. A thorough characterization of the mycovirus is essential before its application. This characterization involves understanding its genetic composition, replication strategy, host range, persistence in the host, mode of transmission, and any potential effects on host biology. These insights are essential to predict mycovirus behavior within the host and evaluate its potential efficacy. By carefully selecting and characterizing mycoviruses, researchers, and growers can better tailor their approaches to effectively manage plant diseases and other specific objectives, maximizing the benefits of mycovirus-based strategies.

Another fundamental aspect is determining the most appropriate method for introducing a mycovirus into the fungal population, which can be done through mycelial grafting, hyphal anastomosis, protoplast fusion, or direct inoculation of viral particles. The application method must ensure efficient transmission and establishment of the mycovirus within the fungal population. Understanding the population dynamics of the fungal pathogen and the mycovirus is also essential, considering factors such as the mycovirus transmission rate, long-term stability, and potential competition with non-infected fungal isolates. Monitoring and maintaining the presence of the mycovirus within the pathogen population are crucial for sustained disease control.

Mycoviruses must be integrated with other disease management strategies for comprehensive control. Combining different strategies will enhance disease control, which may include cultural practices, chemical treatments, resistant crops, or other biocontrol agents. Furthermore, field trials should be conducted to assess the efficacy of mycoviruses, where disease severity, yield, and other relevant parameters should be monitored to evaluate the impact of mycovirus application. Long-term monitoring is essential for ongoing assessment of variations in the efficacy and stability of mycovirus-mediated control.

It is worth noting that the effective use of mycoviruses requires ongoing research and development efforts. Further studies are needed to optimize their application methods, understand their interactions with hosts and the environment, and address challenges such as stability and other potential issues. Collaboration between researchers, industry professionals, and regulatory bodies is crucial to ensure the safe and effective use of mycoviruses in practical settings.

Conclusion

This review addressed the wide diversity of mycoviruses that infect plant-pathogenic fungi, including their taxonomic classification, genome types, and the spectrum of fungal species they infect. Representative examples of mycoviruses in plant-pathogenic fungi and their distinctive features were emphasized, with a particular focus on mycoviruses affecting *Sclerotinia sclerotiorum*. These mycoviruses are especially promising for biocontrol due to a set of unique characteristics in both the mycoviruses and the host fungus. These features make this interaction particularly interesting and effective in terms of biological control. First, mycoviruses that infect *S. sclerotiorum* are often highly specific to their host. This means they can infect and replicate only within *S. sclerotiorum* without harming other organisms. Furthermore, these mycoviruses often exhibit high efficacy

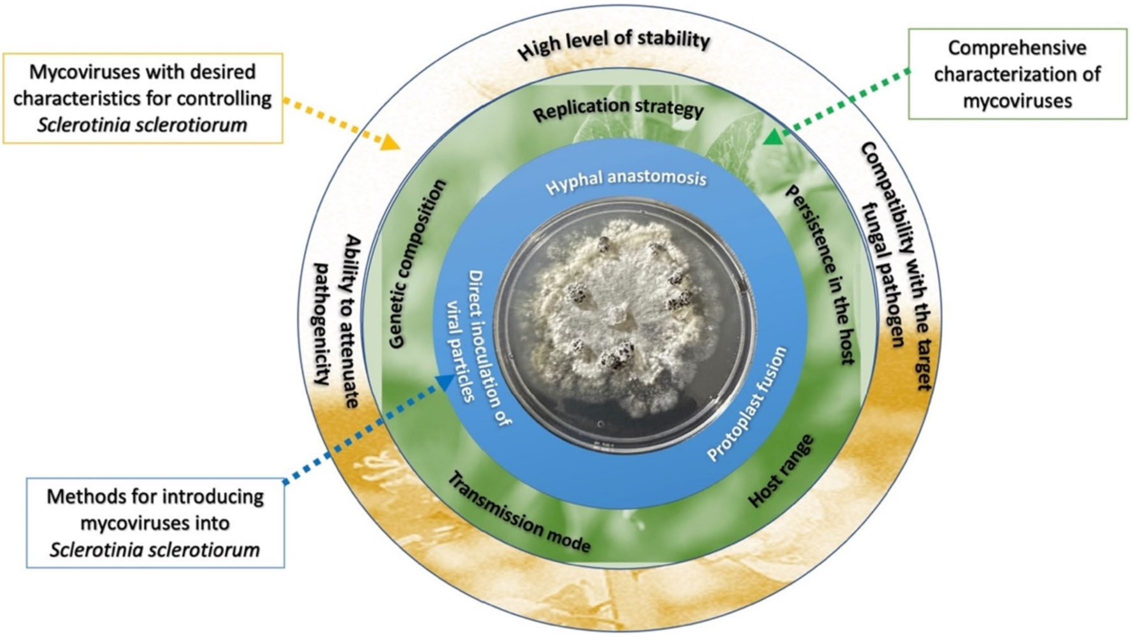

Fig. 5 Key aspects for the characterization, study, and application of mycovirus as a biocontrol strategy for *Sclerotinia sclerotiorum*

in suppressing *S. sclerotiorum* by reducing or eliminating the virulence and reproductive capacity of the fungus, thereby diminishing its ability to cause diseases in host plants. Finally, another important feature is their ability to coexist within the same host for an extended period. This means mycoviruses can persist in the environment alongside *S. sclerotiorum* and continue to serve their biological control function over time.

The remarkable diversity of mycoviruses, coupled with their ability to infect a wide range of plant-pathogenic fungi, inspires optimism. This suggests that these viruses have the potential to serve as effective control strategies against multiple plant pathogens. In addition, mycoviruses are safe for the environment, as they do not pose threats to human health or cause collateral damage to other organisms.

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References

Abdallah I, Yehia R, Kandil MAH (2020) Biofumigation potential of Indian mustard (*Brassica juncea*) to manage *Rhizoctonia solani*. Egypt J Biol Pest Control 30:1–8. https://doi.org/10.1186/s41938-020-00297-y

Abdoulaye AH, Foda MF, Kotta-Loizou I (2019) Viruses infecting the plant pathogenic fungus *Rhizoctonia solani*. Viruses 11(12):1113. https://doi.org/10.3390/v11121113

Ahn IP, Lee YH (2001) A viral double-stranded RNA up regulates the fungal virulence of Nectria radicicola. Mol Plant Microbe Interact 14(4):496–507. https://doi.org/10.1094/MPMI.2001.14.4.496

Allen TD, Dawe AL, Nuss DL (2003) Use of cDNA microarrays to monitor transcriptional responses of the chestnut blight fungus Cryphonectria parasitica to infection by virulence-attenuating hypoviruses. Eukaryot Cell 2(6):1253–1265. https://doi.org/10.1128/EC.2.6.1253-1265.2003

Applen Clancey S, Ruchti F, LeibundGut-Landmann S, Heitman J, Ianiri G (2020) A novel mycovirus evokes transcriptional rewiring in the fungus Malassezia and stimulates beta interferon production in macrophages. Mbio. https://doi.org/10.1128/mBio.01534-20

Azhar A, Mu F, Huang H, Cheng J, Fu Y, Hamid MR, Jiang D, Xie J (2019) A Novel RNA virus related to Sobemoviruses confers hypovirulence on the phytopathogenic fungus *Sclerotinia sclerotiorum*. Viruses 11(8):759. https://doi.org/10.3390/v11080759

Boland GJ (1992) Hypovirulence and double-stranded RNA in *Sclerotinia sclerotiorum*. Can J Plant Pathol 14:10–17. https://doi.org/10.1080/07060669209500900

Boland GJ, Hall R (1994) Index of plant hosts of *Sclerotinia sclerotiorum*. Can J Plant Pathol 16:93–108

Bolton MD, Thomma BP, Nelson BD (2006) *Sclerotinia sclerotiorum* (Lib.) de Bary: biology and molecular traits of a cosmopolitan pathogen. Mol Plant Pathol 7(1):1–16. https://doi.org/10.1111/j.1364-3703.2005.00316.x

Buck KW (1998) Molecular variability of viruses of fungi. In: Molecular variability of fungal pathogens. CAB International, Wallingford, UK 53–72. ISBN: 9780851992662

Castro M, Kramer K, Valdivia L, Ortiz S, Castillo A (2003) A double-stranded RNA mycovirus confers hypovirulence-associated traits to *Botrytis cinerea*. FEMS Microbiol Lett 228(1):87–91. https://doi.org/10.1016/S0378-1097(03)00755-9

Chen B, Gao S, Choi GH, Nuss DL (1994) Extensive alteration of fungal gene transcript accumulation and elevation of G-protein-regulated cAMP levels by a virulence-attenuating hypovirus. Proc Natl Acad Sci USA 93(15):7996–8000. https://doi.org/10.1073/pnas.93.15.7996

Chiba S, Lin YH, Kondo H, Kanematsu S, Suzuki N (2013) Effects of defective interfering RNA on symptom induction by, and replication of, a novel partitivirus from a phytopathogenic fungus *Rosellinia necatrix*. J Virol 87(4):2330–2341. https://doi.org/10.1128/JVI.02835-12

Dean R, Jan AL, Van Kan AL, Pretorius ZA, Hammond-Kosack KE, Di Pietro A, Spanu PD, Rud JJ, Dickman M, Kahmann R, Foster GD (2012) The top 10 fungal pathogens in molecular plant pathology. Mol Plant Pathol 13(4):414–430. https://doi.org/10.1111/J.1364-3703.2011.00783.X

Dilantha FWG, Nakkeeran S, Zhang Y (2004) Ecofriendly methods in combating *Sclerotinia sclerotiorum* (Lib.) de Bary. Recent Res Devel Environ Biol 1: 329–347 ISBN: 81–7736–217–8

Dimkić I, Janakiev T, Petrović M, Degrassi G, Fira D (2022) Plant-associated *Bacillus* and *Pseudomonas* antimicrobial activities in plant disease suppression via biological control mechanisms -A review. Physiol Mol Plant Pathol. https://doi.org/10.1016/j.pmpp.2021.101754

Elderfield JAD, Lopez-Ruiz FJ, van den Bosch F, Cunniffe NJ (2018) Using epidemiological principles to explain fungicide resistance management tactics: Why do mixtures outperform alternations? Phytopathology 108(7):803–817. https://doi.org/10.1094/PHYTO-08-17-0277-R

FAO (2023) Food and Agriculture Organization of United Nations. Available from: https://www.fao.org/faostat/en/#data/QL Cited 21 March 2023

Faruk MI, Rahman MME (2022) Collection, isolation and characterization of *Sclerotinia sclerotiorum*, an emerging fungal pathogen causing white mold disease. J Plant Sci Phytopathol 6:043–051

García-Pedrajas MD, Cañizares MC, Sarmiento-Villamil JL, Jacquat AG, Dambolena JS (2019) Mycoviruses in biological control: from basic research to field implementation. Phytopathology 109(11):1828–1839. https://doi.org/10.1094/PHYTO-05-19-0166-RVW

Ghabrial SA, Suzuki N (2009) Viruses of plant pathogenic fungi. Annu Rev Phytopathol 47:353–384. https://doi.org/10.1146/annurev-phyto-080508-081932

Ghabrial SA, Castón JR, Jiang D, Nibert ML, Suzuki N (2015) 50-plus years of fungal viruses. Virol 479:356–368. https://doi.org/10.1016/j.virol.2015.02.034

Gielen S, Aerts R, Seels B (2004) Biocontrol agents of *Botrytis cinerea* tested in climate chambers by making artificial infection on tomato leafs. Commun Agric Appl Biol Sci 69(4):631–639

Grente J (1965) Les formes hypovirulentes d'Endothia parasitica et les espoirs de lutte contre le chancre du chataignier. CR Acad Agric France 51:1033–1037

Grente J, Berthelay-Sauret S (1978) Research carried out in France into diseases of the chestnut tree. In Proceedings of the American Chestnut Symposium. Eds. West Virginia Univ. Press, Morgantown, WV pp 30–34.

Guetsky R, Shtienberg D, Elad Y, Dinoor A (2001) Combining biocontrol agents to reduce the variability of biological control. Phytopathology 91(7):621–627. https://doi.org/10.1094/PHYTO.2001.91.7.621

Hamid MR, Xie J, Wu S, Maria SK, Zheng D, Assane Hamidou A, Wang Q, Cheng J, Fu Y, Jiang D (2018) A novel Deltaflexivirus that infects the plant fungal pathogen, *Sclerotinia sclerotiorum*, can be transmitted among host vegetative incompatible strains. Viruses 10(6):295. https://doi.org/10.3390/v10060295

Hao F, Ding T, Wu M, Zhang J, Yang L, Chen W, Li G (2018) Two novel hypovirulence-associated mycoviruses in the phytopathogenic fungus *Botrytis cinerea*: molecular characterization and suppression of infection cushion formation. Viruses 10:254. https://doi.org/10.3390/v10050254

Hegedus DD, Rimmer SR (2005) *Sclerotinia sclerotiorum*: When "to be or not to be" a pathogen? FEMS Microbiol Lett 251(2):177–184. https://doi.org/10.1016/j.femsle.2005.07.040

Hiratsuka K, Namba S, Yamashita S, Doi Y (1987) Linear plasmid-like DNAs in the fungus. Botrytis Cinerea JJP 53(5):638–642. https://doi.org/10.3186/jjphytopath.53.638

Hollings M (1962) Viruses associated with dieback disease of cultivated mushrooms. Nature 196:962–965

Hossain MM, Sultana F, Li W, Tran LP, Mostofa MG (2023) Sclerotinia sclerotiorum (Lib.) de Bary: insights into the pathogenomic features of a global pathogen. Cells 12(7):1063. https://doi.org/10.3390/cells12071063

Hough B, Steenkamp E, Wingfield B, Read D (2023) Fungal viruses unveiled: a comprehensive review of mycoviruses. Viruses 15(5):1202. https://doi.org/10.3390/v15051202

Howitt RL, Beever RE, Pearson MN, Forster RL (2001) Genome characterization of Botrytis virus F, a flexuous rod-shaped mycovirus resembling plant 'potex-like'viruses. J Gen Virol 82(1):67–78. https://doi.org/10.1099/0022-1317-82-1-67

Hu Z, Wu S, Cheng J, Fu Y, Jiang D, Xie J (2014) Molecular characterization of two positive-strand RNA viruses co-infecting a hypovirulent strain of *Sclerotinia sclerotiorum*. Virol 464:450–459. https://doi.org/10.1016/j.virol.2014.07.007

Hyder R, Pennanen T, Hamberg L, Vainio EJ, Piri T, Hantula J (2013) Two viruses of *Heterobasidion* confer beneficial, cryptic or detrimental effects to their hosts in different situations. Fungal Ecol 6(5):387–396. https://doi.org/10.1016/j.funeco.2013.05.005

ICTV (2023) Current ICTV Taxonomy Release. Available from: https://ictv.global/taxonomy. Cited 21 March 2023

Jia J, Fu Y, Jiang D, Mu F, Cheng J, Lin Y, Li B, Marzano SL, Xie J (2021) Interannual dynamics, diversity and evolution of the virome in *Sclerotinia sclerotiorum* from a single crop field. Virus Evol. https://doi.org/10.1093/ve/veab032

Kamaruzzaman M, He G, Wu M, Zhang J, Yang L, Chen W, Li G (2019) A novel partitivirus in the hypovirulent isolate QT5-19 of the plant pathogenic fungus *Botrytis cinerea*. Viruses 11:24. https://doi.org/10.3390/v11010024

Khalifa ME, MacDiarmid RM (2021) A mechanically transmitted DNA mycovirus is targeted by the defence machinery of its host *Botrytis cinerea*. Viruses 13(7):1315. https://doi.org/10.3390/v13071315

Khalifa ME, Pearson MN (2013) Molecular characterization of three mitoviruses co-infecting a hypovirulent isolate of *Sclerotinia sclerotiorum* fungus. Virol 441(1):22–30. https://doi.org/10.1016/j.virol.2013.03.002

Khalifa ME, Pearson MN (2014) Characterisation of a novel hypovirus from *Sclerotinia sclerotiorum* potentially representing a new genus within the *Hypoviridae*. Virol 464:441–449. https://doi.org/10.1016/j.virol.2014.07.005

Khan HA, Baig DI, Bhatti MF (2023a) An overview of mycoviral curing strategies used in evaluating fungal host fitness. Mol Biotechnol 65(10):1547–1564. https://doi.org/10.1007/s12033-023-00695-1

Khan HA, Nerva L, Bhatti MF (2023b) The good, the bad and the cryptic: The multifaceted roles of mycoviruses and their potential applications for a sustainable agriculture. Virology 585:259–269. https://doi.org/10.1016/j.virol.2023.07.004

Ko YH, So KK, Chun J, Kim DH (2021) Distinct roles of two DNA methyltransferases from *Cryphonectria parasitica* in fungal virulence, responses to hypovirus infection, and viral clearance. Mbio 12(1):e02890-e2920. https://doi.org/10.1128/mBio.02890-20

Kondo H, Botella L, Suzuki N (2022) Mycovirus diversity and evolution revealed/inferred from recent studies. Annu Rev Phytopathol 60:307–336. https://doi.org/10.1146/annurev-phyto-021621-122122

Kotta-Loizou I (2021) Mycoviruses and their role in fungal pathogenesis. Curr Opin Microbiol 63:10–18. https://doi.org/10.1016/j.mib.2021.05.007

Kotta-Loizou I, Coutts RH (2017) Mycoviruses in *Aspergilli*: a comprehensive review. Front Microbiol 8:1699. https://doi.org/10.3389/fmicb.2017.01699

Kotta-Loizou I, Sipkova J, Coutts RH (2015) Identification and sequence determination of a novel double-stranded RNA mycovirus from the entomopathogenic fungus *Beauveria bassiana*. Arch Virol 160:873–875. https://doi.org/10.1007/s00705-014-2332-8

Lee KM, Yu J, Son M, Lee YW, Kim KH (2011) Transmission of *Fusarium boothii* mycovirus via protoplast fusion causes hypovirulence in other phytopathogenic fungi. PLoS ONE. https://doi.org/10.1371/journal.pone.0021629

Lehner MS, de Paula Júnior TJ, Del Ponte EM, Mizubuti ESG, Pethybridge SJ (2017) Independently founded populations of *Sclerotinia sclerotiorum* from a tropical and a temperate region have similar genetic structure. PLoS ONE. https://doi.org/10.1371/journal.pone.0173915

Lemus-Minor CG, Cañizares MC, García-Pedrajas MD, Pérez-Artés E (2019) Horizontal and vertical transmission of the hypovirulence-associated mycovirus *Fusarium oxysporum* f. sp. *dianthi* virus 1. Eur J Plant Pathol 153:645–650. https://doi.org/10.1007/s10658-018-1554-0

Li H, Fu Y, Jiang D, Li G, Ghabrial SA, Yi X (2008) Down-regulation of *Sclerotinia sclerotiorum* gene expression in response to infection with Sclerotinia sclerotiorum debilitation-associated RNA virus. Virus Res 135:95–106. https://doi.org/10.1016/j.virusres.2008.02.011

Li K, Zheng D, Cheng J, Chen T, Fu Y, Jiang D, Xie J (2016) Characterization of a novel *Sclerotinia sclerotiorum* RNA virus as the prototype of a new proposed family within the order Tymovirales. Virus Res 219:92–99. https://doi.org/10.1016/j.virusres.2015.11.019

Li Y, Li S, Liang Z, Cai Q, Zhou T, Zhao C, Wu X (2022) RNA-seq analysis of *Rhizoctonia solani* AG-4HGI strain BJ-1H infected by a new viral strain of Rhizoctonia solani Partitivirus 2 reveals a potential mechanism for hypovirulence. Phytopathology 112(6):1373–1385. https://doi.org/10.1094/PHYTO-08-21-0349-R

Liu H, Fu Y, Jiang D, Li G, Xie J, Peng Y, Yi X, Ghabrial SA (2009) A novel mycovirus that is related to the human pathogen hepatitis E virus and rubi-like viruses. J Virol 83(4):1981–1991. https://doi.org/10.1128/JVI.01897-08

Liu L, Xie J, Cheng J, Fu Y, Li G, Yi X, Jiang D (2014) Fungal negative-stranded RNA virus that is related to bornaviruses and nyaviruses. Proc Natl Acad Sci USA 111(33):12205–12210. https://doi.org/10.1073/pnas.1401786111

Liu L, Wang Q, Cheng J, Fu Y, Jiang D, Xie J (2015) Molecular characterization of a bipartite double-stranded RNA virus and its satellite-like RNA co-infecting the phytopathogenic fungus *Sclerotinia sclerotiorum*. Front Microbiol 6:406. https://doi.org/10.3389/fmicb.2015.00406

Liu TT, Ye FC, Pang CP, Yong TQ, Tang WD, Xiao J, Shang CH, Lu ZJ (2020) Isolation and identification of bioactive substance 1-hydroxyphenazine from Pseudomonas aeruginosa and its antimicrobial activity. Lett Appl Microbiol 71(3):303–310. https://doi.org/10.1111/lam.13332

Luo X, Jiang D, Xie J, Jia J, Duan J, Cheng J, Fu Y, Chen T, Yu X, Li B, Lin Y (2022) Genome characterization and phylogenetic analysis of a novel endornavirus that infects fungal pathogen *Sclerotinia sclerotiorum*. Viruses 14(3):456. https://doi.org/10.3390/v14030456

Márquez LM, Redman RS, Rodriguez RJ, Roossinck MJ (2007) A virus in a fungus in a plant: three-way symbiosis required for thermal tolerance. Science 315(5811):513–515. https://doi.org/10.1126/science.1136237

Marzano SY, Hobbs HA, Nelson BD, Hartman GL, Eastburn DM, McCoppin NK, Domier LL (2015) Transfection of *Sclerotinia sclerotiorum* with in vitro transcripts of a naturally occurring interspecific recombinant of Sclerotinia sclerotiorum hypovirus 2 significantly reduces virulence of the fungus. J Virol 89(9):5060–5071. https://doi.org/10.1128/JVI.03199-14

Marzano SL, Nelson BD, Ajayi-Oyetunde O, Bradley CA, Hughes TJ, Hartman GL, Eastburn DM, Domier LL (2016) Identification of diverse mycoviruses through metatranscriptomics characterization of the viromes of five major fungal plant pathogens. J Virol 90(15):6846–6863. https://doi.org/10.1128/JVI.00357-16

Meena RS, Kumar S, Datta R, Lal R, Vijayakumar V, Brtnicky M, Sharma MP, Yadav GS, Jhariya MK, Jangir CK et al (2020) Impact of agrochemicals on soil microbiota and management: A review. Land 9(2):34. https://doi.org/10.3390/land9020034

Mehta N (2009) Sclerotinia stem rot – an emerging threat in mustard. Plant Dis Res 24(1):72–73

Moriyama H, Urayama S, Higashiura T, Le TM, Komatsu K (2018) Chrysoviruses in *Magnaporthe oryzae*. Viruses. https://doi.org/10.3390/v10120697

Mu F, Xie J, Cheng S, You MP, Barbetti MJ, Jia J, Wang Q, Cheng J, Fu Y, Chen T, Jiang D (2018) Virome characterization of a collection of *S. sclerotiorum* from Australia. Front Microbiol 11(8):2540. https://doi.org/10.3389/fmicb.2017.02540

Mu F, Jia J, Xue Y, Jiang D, Fu Y, Cheng J, Lin Y, Xie J (2021a) Characterization of a novel botoulivirus isolated from the phytopathogenic fungus *Sclerotinia sclerotiorum*. Arch Virol 166(10):2859–2863. https://doi.org/10.1007/s00705-021-05168-x

Mu F, Li B, Cheng S, Jia J, Jiang D, Fu Y, Cheng J, Lin Y, Chen T, Xie J (2021b) Nine viruses from eight lineages exhibiting new evolutionary modes that co-infect a hypovirulent phytopathogenic fungus. PLoS Pathog. https://doi.org/10.1371/journal.ppat.1009823

Myers JM, James TY (2022) Mycoviruses. Curr Biol 32(4):150–155. https://doi.org/10.1016/j.cub.2022.01.049

Nuss DL (2005) Hypovirulence: mycoviruses at the fungal-plant interface. Nat Rev Microbiol 3:632–642. https://doi.org/10.1038/nrmicro1206

Nuss DL (2010) Mycoviruses. In: cellular and molecular biology of filamentous fungi Wiley Online Library 145–152. ISBN: 9781683671299

O'Sullivan CA, Belt K, Thatcher LF (2021) Tackling Control of a Cosmopolitan Phytopathogen: Sclerotinia. Front Plant Sci. https://doi.org/10.3389/fpls.2021.707509

OwashiY AM, Moriyama H, Arie T, Teraoka T, Komatsu K (2020) Population structure of double-stranded RNA mycoviruses that infect the rice blast fungus *Magnaporthe oryzae* in Japan. Front Microbiol. https://doi.org/10.3389/fmicb.2020.593784

Paudel B, Pedersen C, Yen Y, Marzano SYL (2022) Fusarium Graminearum Virus-1 strain FgV1-SD4 infection eliminates mycotoxin deoxynivalenol synthesis by *Fusarium graminearum* in FHB. Microorganisms 10:1484. https://doi.org/10.3390/microorganisms10081484

Pearson MN, Beever RE, Boine B, Arthur K (2009) Mycoviruses of filamentous fungi and their relevance to plant pathology. Mol Plant Pathol 10(1):115–128. https://doi.org/10.1111/j.1364-3703.2008.00503.x

Pingali PL (2012) Green revolution: impacts, limits, and the path ahead. Proc Natl Acad Sci U S A 109(31):12302–12308. https://doi.org/10.1073/pnas.0912953109

Powell HM, Culbertson CG, McGuire JM, Hoehn MM, Baker LA (1952) A filtrate with chemoprophylactic and chemo-therapeutic action against MM and Semliki Forest viruses in mice. Ant Chemother 2(8):432–434

Ramankutty N, Mehrabi Z, Waha K, Jarvis L, Kremen C, Herrero M, Rieseberg LH (2018) Trends in global agricultural land use: implications for environmental health and food security. Annu Rev Plant Biol 69:789–815. https://doi.org/10.1146/annurev-arplant-042817-040256

Ran H, Liu L, Li B, Cheng J, Fu Y, Jiang D, Xie J (2016) Co-infection of a hypovirulent isolate of *Sclerotinia sclerotiorum* with a new botybirnavirus and a strain of a mitovirus. Virol J 13:92. https://doi.org/10.1186/s12985-016-0550-2

Raveau R, Fontaine J, Lounès-Hadj Sahraoui A (2020) Essential oils as potential alternative biocontrol products against plant pathogens and weeds: a review. Foods 9(3):365

Ruiz-Padilla A, Rodríguez-Romero J, Gómez-Cid I, Pacifico D, Ayllón MA (2021) Novel mycoviruses discovered in the mycovirome of a necrotrophic fungus. Mbio. https://doi.org/10.1128/mBio.03705-20

Salinas RN, Martínez PG, Uribe CJ, Romero SRD, García LE, Soto MJJG, Castillo MA, Gutiérrez RA (2022) FAO, FIDA, OMS, PMA y UNICEF. El estado de la seguridad alimentaria y la nutrición en el mundo 2019. Protegerse frente a la desaceleración y el debilitamiento de la economía (primera edición. Roma: FAO, 2019). Revista de Ciencias Sociales (Cr) 1(175):189–193.

Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A (2019) The global burden of pathogens and pests on major food crops. Nat Ecol Evol 3:430–439. https://doi.org/10.1038/s41559-018-0793-y

Shah UA, Kotta-Loizou I, Fitt BD, Coutts RH (2020) Mycovirus-induced hypervirulence of *Leptosphaeria biglobosa* enhances systemic acquired resistance to *Leptosphaeria maculans* in *Brassica napus*. Mol Plant Microbe Interact 33(1):98–107. https://doi.org/10.1094/MPMI-09-19-0254-R

Sharma M, Guleria S, Singh K, Chauhan A, Kulshrestha S (2018) Mycovirus associated hypovirulence, a potential method for biological control of *Fusarium* species. Virusdisease 29:134–140. https://doi.org/10.1007/s13337-018-0438-4

Shi L, Wang J, Quan R, Yang F, Shang J, Chen B (2019) CpATG8, a Homolog of Yeast Autophagy Protein ATG8, Is Required for Pathogenesis and Hypovirus Accumulation in the Chest Blight Fungus. Front Cell Infect Microbiol 9:222. https://doi.org/10.3389/fcimb.2019.00222

Shope RE (1953) An antiviral substance from Penicillium funiculosum: I. Effect upon injection in mice with swine influenza virus and Columbia SK encephalomyelitis virus. J Ex Med 97(5):601–625. https://doi.org/10.1084/jem.97.5.601

Son M, Yu J, Kim KH (2015) Five questions about mycoviruses. PLoS Pathog. https://doi.org/10.1371/journal.ppat.1005172

Sukphopetch P, Suwanmanee S, Pumeesat P, Ampawong S (2021) In vitro characterization of Chrysovirus-1-induced hypovirulence of *Bipolaris maydis*. Walailak J Sci and Tech 18(3):6564–6568

van den Berg F, van den Bosch F, Paveley ND (2013) Optimal fungicide application timings for disease control are also an effective anti-resistance strategy: a case study for *Zymoseptoria tritici* (*Mycosphaerella graminicola*) on wheat. Phytopathology 103(12):1209–1219. https://doi.org/10.1094/PHYTO-03-13-0061-R

van Diepeningen AD, Varga J, Hoekstra RF, Debets AJ (2008) Mycoviruses in aspergilli. Aspergillus in the genomics era. WAP 133–176. ISBN: 9789086860654

van Diepeningen AD (2021) Biocontrol via mycoviruses: a neglected option for bioprotection? In: Microbial bioprotectants for plant disease management. Burleigh Dodds Science Publishing 15:541–584 ISBN (Print) 9781786768131

Van Dijk M, Morley T, Rau ML, Saghai Y (2021) A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. Nat Food 2:494–501. https://doi.org/10.1038/s43016-021-00322-9

Villan Larios DC, Diaz Reyes BM, Pirovani CP, Loguercio LL, Santos VC, Góes-Neto A, Fonseca PLC, Aguiar ERGR (2023) Exploring the mycovirus universe: identification, diversity, and biotechnological applications. J Fungi 9(3):361. https://doi.org/10.3390/jof9030361

Wang M, Wang Y, Sun X, Cheng J, Fu Y, Liu H, Jiang D, Ghabrial SA, Xie J (2015) Characterization of a novel megabirnavirus from *Sclerotinia sclerotiorum* reveals horizontal gene transfer from single-stranded RNA virus to double-stranded RNA virus. J Virol 89(16):8567–8579. https://doi.org/10.1128/JVI.00243-15

Wang Q, Mu F, Xie J, Cheng J, Fu Y, Jiang D (2020) A Single ssRNA segment encoding RdRp is sufficient for replication, infection, and transmission of ourmia-Like virus in fungi. Front Microbiol 11:379. https://doi.org/10.3389/fmicb.2020.00379

Wang Y, Xu Z, Hai D, Huang H, Cheng J, Fu Y, Lin Y, Jiang D, Xie J (2022) Mycoviromic analysis unveils complex virus composition in a hypovirulent strain of *Sclerotinia sclerotiorum*. J Fungi 8(7):649. https://doi.org/10.3390/jof8070649

Williamson B, Tudzynski B, Tudzynski P, van Kan JA (2007) *Botrytis cinerea*: the cause of grey mould disease. Mol Plant Pathol 8:561–580. https://doi.org/10.1111/j.1364-3703.2007.00417.x

Wu M, Zhang L, Li G, Jiang D, Ghabrial SA (2010) Genome characterization of a debilitation-associated mitovirus infecting the phytopathogenic fungus Botrytis cinerea. Virology 406(1):117–126. https://doi.org/10.1016/j.virol.2010.07.010

Wu S, Cheng J, Fu Y, Chen T, Jiang D, Ghabrial SA, Xie J (2017) Virus-mediated suppression of host non-self-recognition facilitates horizontal transmission of heterologous viruses. PLoS Pathog. https://doi.org/10.1371/journal.ppat.1006234

Xiao X, Cheng J, Tang J, Fu Y, Jiang D, Baker TS, Ghabrial SA, Xie J (2014) A novel partitivirus that confers hypovirulence on plant pathogenic fungi. J Virol 88(17):10120–10133. https://doi.org/10.1128/JVI.01036-14

Xie J, Ghabrial SA (2012) Molecular characterizations of two mitoviruses co-infecting a hypovirulent isolate of the plant pathogenic fungus *Sclerotinia sclerotiorum*. Virol 428(2):77–85. https://doi.org/10.1016/j.virol.2012.03.015

Xie J, Jiang D (2014) New insights into mycoviruses and exploration for the biological control of crop fungal diseases. Annu Rev Phytopathol 52:45–68. https://doi.org/10.1146/annurev-phyto-102313-050222

Xie J, Wei D, Jiang D, Fu Y, Li G, Ghabrial S, Peng Y (2006) Characterization of debilitation-associated mycovirus infecting the plant-pathogenic fungus *Sclerotinia sclerotiorum*. J Gen Virol 87(1):241–249. https://doi.org/10.1099/vir.0.81522-0

Xie J, Xiao X, Fu Y, Liu H, Cheng J, Ghabrial SA, Li G, Jiang D (2011) A novel mycovirus closely related to hypoviruses that infects the plant pathogenic fungus *Sclerotinia sclerotiorum*. Virology 418(1):49–56. https://doi.org/10.1016/j.virol.2011.07.008

Xu Z, Wu S, Liu L, Cheng J, Fu Y, Jiang D, Xie J (2015) A mitovirus related to plant mitochondrial gene confers hypovirulence on the phytopathogenic fungus *Sclerotinia sclerotiorum*. Virus Res 197:127–136. https://doi.org/10.1016/j.virusres.2014.12.023

Ye T, Lu Z, Li H, Duan J, Hai D, Lin Y, Xie J, Cheng J, Li B, Chen T, Fu Y, Jiang D (2023) Characterization of a fungal virus representing a novel genus in the family *Alphaflexiviridae*. Viruses 15(2):339. https://doi.org/10.3390/v15020339

Yu X, Li B, Fu Y, Jiang D, Ghabrial SA, Li G, Peng Y, Xie J, Cheng J, Huang J, Yi X (2010) A geminivirus-related DNA mycovirus that confers hypovirulence to a plant pathogenic fungus. PNAS 107(18):8387–8392. https://doi.org/10.1073/pnas.0913535107

Yu X, Lia B, Fu Y, Xie J, Cheng J, Ghabrial SA, Lia G, Yi J, Jiang D (2013) Extracellular transmission of a DNA mycovirus and its use as a natural fungicide. PNAS 110(4):1452–1457. https://doi.org/10.1073/pnas.1213755110

Zhang DX, Nuss DL (2016) Engineering super mycovirus donor strains of chestnut blight fungus by systematic disruption of multilocus vic genes. Proc Natl Acad Sci USA 113(8):2062–2067. https://doi.org/10.1073/pnas.1522219113

Zheng L, Lu X, Liang X, Jiang S, Zhao J, Zhan G, Liu P, Wu J, Kang Z (2017) Molecular characterization of novel totivirus-like double-stranded RNAs from *Puccinia striiformis* f. sp. tritici, the causal agent of wheat stripe rust. Front Microbiol 8:1960. https://doi.org/10.3389/fmicb.2017.01960

Zheng L, Zhao J, Xiaofei Liang X, Zhuang H, Qi T, Kang Z (2019) Complete genome sequence of a novel mitovirus from the wheat stripe rust fungus *Puccinia striiformis*. Arch Virol 164:897–901. https://doi.org/10.1007/s00705-018-04134-4

Zhou L, Li X, Kotta-Loizou I, Dong K, Li S, Ni D, Hong N, Wang G, Xu W (2021) A mycovirus modulates the endophytic and pathogenic traits of a plant associated fungus. ISME J 15(7):1893–1906. https://doi.org/10.1038/s41396-021-00892-3