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Mycoviruses: trends in plant-fungus-mycovirus interactions and 'biocontrol' prospects in agriculture and the environment

Elias Mjaika NDIFON [1, 2], Gilbert Nchongboh CHOFONG [3]

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Abstract: Mycoviruses are cosmopolitan in plants, animals, fungi, bacteria, in soils, and water. There is a scarcity of information about them, which necessitated this review to provide some leads on where research should focus. Mycoviruses are able to persist in disparate types of hosts by utilizing diverse measures. They may engage either parasitic, pathogenic, or mutualistic tendencies. Mycoviruses employ many existential strategies that can be utilized by man. Hypovirulence may be induced in fungal hosts by mycoviruses via RNA silencing, alteration of genetic expression, and disruption of the transcriptome. Mycoviruses interact with killer phenotypes of yeasts and *Ustilago* spp. and proffer advantages to these fungi. Mycovirus interaction with some plants result in provision of thermal tolerance to plants. Based on their mode of microbe destruction mycoviruses may be used for waste disposal and termination of some life processes. For instance, grazer viruses completely oxidize the organic content of their host into carbon dioxide and inorganic nutrients, while lytic viruses release the organic material from their hosts without modification. Viruses may be utilized to facilitate the exchange of genetic material from one host to another. However, pathogenic mycoviruses exist especially in mushrooms.

Key words: control, disease complex, fungi synergy, integrated pest management, phage, relationship

Mikovirusi: trendi v interakcijah rastlina-gliva-mikovirus in izgledi 'biokontrole' v kmetijstvu in okolju

Izvleček: Mikovirusi so kozmopoliti v rastlinah, živalih, glivah, bakterijah, v tleh in vodi. O njih je le malo informacij, kar je bilo vodilo za ta pregled kot smernico za bodoče raziskave. Mikovirusi so sposobni bivati v različnih gostiteljih z različnimi načini preživetja. Uporabljajo lahko zajedalske, patološke ali mutualistične strategije, ki jih lahko koristimo tudi ljudje. Hipovirulenca je v glivnem gostitelju lahko vzpodbujena z mikovirusi preko RNA utišanja, spremembe izražanja genov in razgradnje transkriptoma. Mikovirusi sodelujejo z ubijalskimi fenotipi kvasovk in sneti (*Ustilago* spp.), kar daje prednosti tem glivam. Sodelovanje mikovirusov in nekaterih rastlin rezultira v njihovi toleranci na termperaturne spremembe. Na osnovi njihovega uničevanja mikrobov bi lahko mikoviruse uporabili za razgradnjo odpadkov in za zaključek nekaterih bioloških procesov. Na primer, virusi, ki se "pasejo" na mikrobih (grazer viruses) popolnoma oksidirajo organsko vsebino gostitelja do ogljikovega dioksida in anorganskih hranil med tem, ko litični virusi sproščajo organske snovi iz njihovih gostiteljev. Virusi se lahko uporabljajo za olajševanje izmenjave dednine iz enega gostitelja v drugega. Še posebej veliko patogenih mikovirusov živi v gobah.

Ključne besede: nadzor, bolezenski kompleks, glivno sodelovanje, integrirano uravnavanje škodljivcev, fag, odnosi

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[1] Alex Ekwueme Federal University Ndufu-Alike, Faculty of Agriculture, Department of Crop Science, Abakaliki, Nigeria
[2] Corresponding author, e-mail: emndi4nn@yahoo.com
[3] Julius Kühn Institut, Federal Research Centre for Cultivated Plants, Institute for Epidemiology and Pathogen Diagnostics, Braunschweig, Germany

1 INTRODUCTION

The discovery of bacteriophages and ultimately of mycoviruses/mycophages has been a great leap forward for researchers. Mycoviruses (mycophages) are a group of viruses that are naturally associated with fungi (including fungi associated with plants, mushrooms, microbes, soil, and water) (SDSU, 2021; Hu et al., 2022). Mycoviruses interact with four phyla of true fungi (eufungi): the Chytridiomycota (chytrids), Zygomycota (bread molds), Ascomycota (yeasts and sac fungi), and the Basidiomycota (club fungi). The relation of myoviruses with Pseudofungi like those in the Phyla Oomycota and Hyphochytridiomycota (in Kingdom Chromista i.e. some water moulds or Straminipila) and as well as slime moulds - other fungi-like organisms (Ghabrial and Suzuki, 2009; Pearson et al., 2009; Beakes et al., 2014; Xie and Jiang, 2014; Zhong et al., 2016; Calvalier-Smith, 2018; Myers et al., 2020; Zhou et al., 2021; Hough et al., 2023) was not covered in this review. Fungi are frequently infected with two or more unrelated viruses (Ghabriel and Suzuki, 2008; Howitt et al., 2006). Fungi may also act as vectors of viruses of higher life forms (Adams, 1991). The mycovirus-host fungus relationship take the form of mutualistism, commensalism, or parasitism.

Viruses associated with fungi or mycoviruses associated with higher life forms usually do not induce symptoms in their host fungi, except in the case of hypervirulence (increase in virulence of the symptoms of the infection of the fungus on its host: extremely or unusually virulent) and hypovirulence (decrease of the symptoms of the infection of the fungus on its host: extremely or unusually reduced virulence) (Ghabrial and Suzuki (2009). On the other hand, the diseases on some fungi and mushrooms/macrofungi are caused by the mycoviruses themselves. Ghabrial and Suzuki (2009) reported that mycoviruses are associated with latent infections of all major groups of plant pathogenic fungi. Some mycoviruses cause debilitating diseases and/or reduce the virulence of their phytopathogenic fungal hosts and these may lead to attenuation (hypovirulence) or enhancement of fungal virulence (hypervirulence).

Kong et al. (1997), Nuss (2005), Ong et al. (2016), García-Pedrajas et al. (2019), and Siddique (2020) reiterated that some mycoviruses reduce the virulence of the host fungus (hypovirulence), which can make the fungus less harmful to plants, whereas other mycoviruses have been shown to enhance the virulence of the host fungus (hypervirulence). However mycoviruses may be pathogenic on their hosts.

For instance, la France virus disease of cultivated mushrooms (*Agaricus bisporus* (J.E. Lange) Pilat was first reported in the late 1940s (Hollings, 1962; Ghabrial and Suzuki, 2009). Alvarez-Jubete et al. (2011) reported that Mushroom Virus X affects important traits associated with mushroom quality (including colour and appearance). Another instance is the effective virus-control of chestnut blight (caused by the fungus - *Cryphonectria parasitica* (Murrill) M.E. Barr) as a consequence of the infection of the fungus by the mycovirus - *Cryphonectria parasitica* hypovirus 1 (CHV1) in Europe (Hollings, 1962).

The natural distribution of mycoviruses seems to follow a normal distribution spectrum with avirulent, mutualistic, and virulent members being commonplace. Many mycoviruses have been shown to be mutualists.

Mycoviruses can alter host's tolerance to environmental stresses, e.t.c. Most of these mycoviruses have not been described to date or are unrelated to any known viruses. According to the PVEN (Plant Virus Ecology Network) (2011) viruses are widely distributed entities that can cause substantial mortality of plants and animals. Secondly, viruses can move genetic elements between hosts e.g. potentially between genetically engineered plants and non-target species.

Studies of host–mycovirus–vector interactions in nature offer both opportunities and challenges that will ultimately produce multi-faceted understanding of the role of mycoviruses in shaping ecological and evolutionary dynamics (Fargette et al., 2006; PVEN, 2011). Studies of pathogenic viruses have probably left out a vast majority of viruses. Mycovirus diversity is another area of mycovirology that has barely been explored. Virtually all plant (and perhaps all animal) species harbor pathogenic or mutualistic fungi in their tissues.

Kotta-Loizou (2019) pointed out that our current understanding of mycoviruses is not as detailed as in other fields of virology and currently not based on cutting-edge methodology. The general assumption is that much information is yet to be generated on mycoviruses especially considering that the majority of these mycoviruse are viruses of microorganisms (VOMs). With the advent of high-throughput sequencing and bioinformatics analysis pipelines in mycovirology, different types of mycoviruses are being discovered in all the four phyla of true fungi. Recent research has revealed an unexpected diversity of these mycoviruses, their interactions with plants, and modulation of some plant biotic and abiotic stresses.

Mycoviruses can be useful in molecular biology and biotechnology. We are just beginning to tap this potential. This appraisal was set up to document the literature on mycoviruses, diversity of currently known host-parasite interactions and biocontrol prospects possible in agriculture and the environment.

2 PLANT-FUNGI-MYCOVIRUS INTERACTIONS

Recently, researchers reported that viruses are the most abundant and dynamic entities in the hydrosphere (Weinbauer, 2004; Suttle, 2007) although Payet et al. (2014) contested that little is known about viruses in these water habitats. Viruses are major agents of microbial mortality and account for about 50% of bacterial mortality in the hydrosphere (Kirchman, 2018). Daily, between 20–50% of heterotrophic bacteria, cyanobacteria and phytoplankton are infected by viruses (Brussaard, 2004; Suttle, 2007).

Viral lysis releases organic cellular content and nutrients necessary for autotrophic and heterotrophic microbial life forms (Shelford et al., 2012). This essentially result in major changes in the biogeochemical nutrient (carbon, nitrogen and phosphorus) cycles and flow of energy in the oceans (Suttle, 2007; O‘Malley, 2016). Kirchman (2018) stated that apparently viruses infecting fungi do not lyse their host and are rather transmitted from one fungus to another intracellularly, without being released into the external environment.

True mycoviruses demonstrate an ability to be transmitted and infect other still healthy fungi cells. The interaction between the mycovirus (*Cryphonectria parasitica* hypovirus 1 (CHV1)) with *Cryphonectria parasitica* (the causative agent of chestnut blight)), in Europe resulted in hypovirulence in the fungus. Thus the blight was controlled whenever a virulent strain of the virus attacked the plant.

However, this ‘biocontrol’ is restricted to a small number of plant vegetation compatibility groups (pVCGs). For instance, in North America plant vegetation incompatibility reactions prevent plant roots from fusing and exchanging their cytoplasmic content, thus hypovirulent strains of mycoviruses are hindered from spreading (See Anagnostakis et al., 1998). Hence in the USA, China and Japan this ‘biocontrol’ measure tends to fail due to a large number of different plant VCGs (Liu and Milgroom, 2007).

The natural host range of a mycovirus is supposed to be confined to taxa performing cytoplasmic fusion (Buck, 1986) but some mycoviruses can replicate in unrelated taxa not allowing anastomosis of the fungal hyphae. This is the case with two fungal species (*Sclerotinia homoeocarpa* Benn. and *Ophiostoma novo-ulmi* Braiser*)* associated with chestnut tree (Deng and Boland, 2003; Nuss et al., 2005). Chen et al. (1994) extended the natural host range of CHV1 to several phylogenetically unrelated fungal species associating with chestnut and supported their hypothesis using *in vitro* virus transfection techniques. In line with this, CHV1 can also propagate in the genera *Endothia* Murrill species (Cryphonectriaceae) and *Valsa* Fr. species (Diaporthales, Valsaceae) (Ghabriel and Suzuki, 2008).

Various studies revealed that the same mycovirus can be transmitted between different species of the same genus found in the same habitat. For instance the same mycovirus was transmitted between *Cryphonectria* spp. (i.e.; *Cryphonectria parasitica* and *Cryphonectria* sp.), *Sclerotinia* spp. (i.e.; *Sclerotinia sclerotiorum* (Lib.) de Bary and *Sclerotinia minor* Jagger), and *Ophiostoma* spp. (*Ophiostoma ulmi* (Buism.) Nannf. syn. *Ceratocystis ulmi* (Buism.) C. Moreau and *Ophiostoma novo-ulmi*) (Liu et al., 2003; Melzer et al., 2005).

Moreover, interspecies transmission has been reported between *Fusarium poae* (Peck) Wollenw and *Aspergillus* species (van Diepeningen et al., 2006). The mode of transmission in these instances is unknown and is still subject to guess work. Mycovirus infections are common even in humans as is the case with the mycoviruses in *Aspergillus fumigatus* Fresenius (i.e. AfuPmV-1) and *Talaromyces marneffei* Segretain, Capponi & Sureau) Samson, Yilmaz, Frisvad & Seffert (i.e. TmPV1) (Kotta-Loizou and Coutts, 2017; Lau et al., 2018).

Research on mycoviruses is hindered by many factors amongst which is the lack of appropriate infectivity assays (McCabe et al., 1999) and mixed infection or unknown numbers of infecting viruses. These situations make it difficult to ascribe a particular phenotypic change in the host to a particular virus under investigation. Moreover, neutral co-existence (likely due to co-evolutionary processes) may be in operation in a virus-fungus interaction (Araújo et al., 2003). These difficulties have hindered the studies on hypovirulent strains of mycoviruses. This is often due to lack of correlation between phenotypes and specific genomes or particular metabolic pathways (Xie et al., 2006).

Equilibrium offsetting conditions could also be responsible for changes in host-parasite relationships. Possibly, this is due to changes from mutual to neutral then to deleterious, and so on. Other relationships exist in the same habitat. Vidhyasekaran (2004) reported that satellite viruses are dependent on other viruses to supply the enzyme replicase and other enzymes necessary for replication. A satellite virus associated with Tobacco necrosis is not serologically related to Tobacco necrosis virus (TNV). TNV multiply indefinitely without causing the production of a satellite virus. However, the satellite virus is entirely dependent on TNV for its multiplication. The satellite virus has a viral coat and a small genome of its own. Both viruses are transmitted among roots by the fungus *Olpidium brassicae* (Woronin) P.A. Dang.

Sometimes satellite viruses also have satellite RNAs e.g., the satellite of Tobacco necrosis virus (TNV) has a small satellite RNA that is dependent on Tobacco necrosis virus for replication and on the satellite virus for encapsulation (Vidhyasekaran, 2004). Moreover, various plant viruses (of the Tombusviridae) generate defective interfering RNA viruses during replication (Rubio et al., 1999). This new relationship may result in viral symptom amelioration (Roux et al., 1991; Kong et al., 1997) or intensification as observed in the case of the Turnip crinkle virus (Li et al., 1989; Kong et al. 1997). Hough et al. (2023) stated that mycoviruses have the ability to reduce the virulence of their hosts.

Rowley (2016), and Moonil et al. (2015) reported that asymptomatic associations with fungi and by mycoviruses are very common. Furthermore, fungi are often associated with unrelated viruses or 'defective dsRNA' and/or satellite dsRNA (Howitt et al., 2006; Ghabrial and Suzuki, 2009). Moreover, some viruses simply use fungi as vectors (which differentiate them from mycoviruses) since they do not replicate inside the fungus (Adams, 1991).

Tran et al. (2019) reported that very little is known about mycoviruses infecting *Monilinia* species although virus-like particles (VLPs) resembling those of partitiviruses, totiviruses, tobraviruses, and furoviruses have been reported from these hosts. McCabe et al. (1999) and Rowley (2016) argued that the virulence of a virus is ultimately limited by the need for the host to survive and thus permit the virus to replicate and continue to exist. This has not been proven.

Based on the obligate parasitic nature of viruses, the majority of mycoviruses should have some negative effect(s) on fungal growth or survival. This depends on the mode of infection and the population of the viruses. More than 250 mycoviruses infect true fungi in the aforementioned phyla (Bozarth, 1972; Rochon et al., 2004; Hacker et al., 2005; Ghabrial and Suzuki, 2009; Rowley, 2016; Tran et al., 2019; Xia et al., 2020). Many viruses can simultaneously infect a single fungus (Hollings, 1962).

Based on O'Malley (2016) viruses may operate in hosts with or without being pathogenic. De Filippis and Villarreal (2000) stated that a competition between different viral strains or individuals inside a host may result in selection of the fittest. Viruses have both general and specific requirements for replication and existence. The direction and extent of this change is determined by a combination of stochastic and environmental factors that are specific for a given time, space, and taxon.

Though viruses of plants have long been recognized as important components of plant ecosystems, only a few notable mycovirus have been studied in detail. Marzano et al. (2015) reported that a comprehensive picture of mycoviral diversity is lacking. Tran et al. (2019) lamented that the influence of mycoviruses on the ecosystem has not been well studied. For instance, the lack of studies on how some mycoviruses reduce the ability of their fungal host to cause plant diseases. Besides, it has been assumed that the natural host range of mycoviruses is confined to closely related vegetation-compatibility groups (VCGs) which allow fusion of cytoplasm (Buck, 1986). These assumptions may or may not be true, and are based on assumptions.

Zhang et al. (2020) attested that it is unclear how mycovirus that cause hypovirulence prevail in the field. Myers and James (2022) suggested the presence of mutualism between mycoviruses and their hosts. Pearson et al. (2009) agreed that our understanding of the interaction between mycoviruses and their hosts is largely limited to a few well-studied, possibly atypical systems. Coupled with the problem of mixed infections by multiple viruses (for example the mixed infection of *Botrytis cinerea* virus F (*BCVF*) and Botrytis virus X (*BVX*) in *Botrytis cinerea* Pers.) it may not be easy to ascribe a definite role to a mycovirus (Howitt et al., 2006). De Filippis and Villarreal (2000) emphasized that viral infection of a host may not necessarily involve tissue destruction, mortality or even full/partial mobilization of host antiviral mechanisms. Indeed, virus association with hosts may result in mutualistic relationships.

Most mycoviruses do not cause symptomatic infections in their hosts (Ghabrial et al., 2015; Khan et al., 2022). Symptom expression usually occur when there is hypersensitive reaction or incompatibility of the host and parasite. Rowley (2016) reported that fungal hosts defend themselves from mycoviruses using RNA interference (RNAi), which inhibit mycovirus replication. This may result in cell death thus blocking mycovirus transmission. De Filippis and Villarreal (2000) reported that disabling antiviral systems in fungi improves the chances of virus continuity. Bacteria hosts can employ abortive infection as a last resort to escape from the effects of bacteriophages (Weinbauer 2004). However, many mycoviruses interfer with fungal RNAi to prevent the inhibition of their replication. Interactions between vegetatively incompatible plants and fungal isolates culminate in programmed cell death (PCD) thus hindering any exchange of infected cellular contents (Nuss, 2011).

Biella et al. (2002) affirmed that mycovirus infection is influenced by the rate of PCD which could mean that mycoviruses may have developed mechanisms for delaying or hindering occurrence of PCD. RNA silencing (as a defence mechanism in fungi) invoked by fungi against viruses may be made inefficient by some viruses including mycoviruses (Segers et al., 2007). Furthermore, Moonil et al. (2015), and Rowley (2016) pointed out that some mycoviruses are associated with killer satellite virus particles which induce their fungus host to secrete toxins that kill competing fungi. This host fungus beneficial mechanism is exhibited by the budding yeasts (*Sacharomyces cerevisiae* (Desm.) Meyen) in fermented foodstuffs.

These dsRNA satellite viruses are dependent on the Totiviridae mycoviruses for their stability. Alone, totiviruses have a minimal impact upon *S. cerevisiae*, but the additional presence of satellite RNAs provide additional capabilities to the virus which is an important example of a beneficial virus system. In fact, these killer systems are so beneficial to their hosts that in some cases, they have resulted in the loss of host RNAi systems (Drinnenberg et al., 2011; Moonil et al., 2015). Thus symptomless or latent mycoviruses may have unknown functions in their hosts. Somehow, some mycoviruses may act as extra-chromosomal genes that confer an advantage to the host as can be observed with the killer systems in yeast (Schmitt and Breinig, 2006).

Another example of beneficial relationship with a mycovirus, is a three-way symbiosis (among a mycovirus, an endophytic fungus, and tropical panic grass). The endophytic fungus (*Curvularia protuberata* Boedijn), panic grass (*Dichanthelium lanuginosum* (Elliott) Gould), and other plants can only survive high soil temperatures in the presence of the mycovirus (Márquez et al., 2007; Moonil et al., 2015). The mycovirus in turn obtains its basic necessities from its hosts. The mechanisms involves two distinct viral dsRNAs. A mutualistic relationship is also found in an interaction among *Trichoderma* Pers. species and their mycoviruses, and the host plant (Beilei et al., 2020).

The fungus is required for thermal tolerance of the plants. A parasite often tend to reduce its impact on its host, thus many parasites have co-evolved to an equilibrium state resulting in minimal impact. Therefore there is great variability in reactions between a single host and different viruses or dsRNAs.

Furthermore, Khan et al. (2022) reported that several types of virus-virus interactions (i.e.; synergistic, antagonistic, and mutualistic interactions) have been reported in fungal hosts. Co-infections of single fungal strains by over ten mycoviruses has been reported for several phytopathogenic fungi, which implies that much work has to be carried out to determine the type of relathionships that are created in such co-infections.

The effects of a mycovirus seems to be dependent on other factors like environment and presence of other invaders. For instance, Chu et al. (2002) reported a wide spectrum of reactions: reduced growth, increased pigmentation, reduced virulence, and a 60-fold decreased production of trichothecene mycotoxins associated with a dsRNA during a study of *Fusarium graminearum* Schwabe (syn *Gibberella zeae* (Schwein.) Petch) on wheat. Fine (1975) assumed that mycoviruses may be unable to persist if they lower the fitness of their hosts, because they are limited to vertical transmission only. In a detailed study of the effects of dsRNA on the fitness of asexual *Aspergillus* species, no beneficial effects were observed (Van Diepeningen et al., 2006) in vitro. In contrast Tran et al. (2007) observed higher growth rates of BVX-infected fungus compared to the same uninfected isolate.

It has been postulated that the virus environment is both multidimensional and continually changing thus constantly driving the increase in population fitness. It could also be argued that based on quantity of variables in the environment, viruses exhibit greater mobility through the space of their selective or adaptive environments than do more complex organisms (Moya, 1997).

De Filippis and Villarreal (2000) reported that the many levels of viral characters (point mutations, coding region products, multigene assemblages, behavioral traits, and even populational characters) can be considered as adaptations and may all endow their possessors with replication advantages. The adaptive viral characters favored within the relatively closed system of one individual host arise and persist due to intra-host selection pressure, the nature and strength of which is determined by the environmental conditions and other virus strains contained therein.

De Filippis and Villarreal (2000) reported that the host's cellular, tissue, and organismal environments are vitally important selective realms that contribute profoundly to the adaptation and diversity of viruses including mycoviruses. Also by disabling antiviral systems the virus reduces its own population decline. In the ecosystem the fittest mycovirus optimizes its utilization of host resources and does not maximize the utilization of host resources. This permits them to continue to persist despite the intrahost selection pressure. Thus the fittest individuals are not the ones that maximizes the use of host resources, rather the fittest individuals are those that optimizes the utilization of host resources.

To ensure continuity in most viral infections, less than 1 % of the susceptible host tissue is actually infected/harvested (Griffin, 1997). Such a host-parasite interaction could persist and be observed as any of the forms of guilds depending on the colorations and flavours added to it. In micro-ecosytems, the essential portion of the environment that is of most concern is the inorganic nutrients and energy derivable from the hosts. The mycovirus should therefore be properly adapted to avoid depleting these resources unnecessarily. In the case of bacteriophages, they impact the movement of nutrients and energy within the micro-ecosystems primarily by lysing bacteria and secondarily by encoding of exotoxins (a subset of which are capable of solubilizing the biological tissues of living hosts/animals) (Weinbauer, 2004). Much has been reported already about viruses of plants, humans and animals so this will only be discussed briefly as antagonistic components of the micro-ecostystem. Kazinczi et al. (2004) pointed out that weeds, as alternative hosts of plant viruses can act as alternative nutrient sources for viruses and virus vectors. Weeds play important role in virus ecology and epidemiology. Alemu et al. (2002) reported that chronic infection with viruses is a major constraint that often force farmers to ban hot pepper production. This can result in decrease in the population of virus and mycovirus entities in an area. The presence of infected weeds throughout the year means, that they are reservoirs and sources of viruses for secondary spread. Yudin et al. (1986) reported that western flower thrips (*Frankliniella occidentalis* Pergande, 1895 - a known vector of tomato spotted wilt virus, was found to be associated with 48 plant species growing within the Kula vegetable-growing region on the island of Maui, Hawaii. This type of vector can be very vital for continual existence of mycoviruses even when the host plant and fungus are facing difficult times in the dry season. Weeds are widely infected by viruses. For instance, McGovern et al. (2008) reported that *Solanum viarum* Dunal (the invasive tropical soda apple) in Florida was infected by nine viruses which can in turn infect solanaceous crops.

3 IMPLICATION OF MYCOVIRUS INTERACTIONS WITH PLANTS IN CROP PROTECTION: TRENDS IN RESEARCH, APPLICATIONS, AND 'BIOLOGICAL' CONTROL POTENTIALS USING THESE AGENTS

We have just seen how the killer phenotypes can provide some advantages to yeasts and *Ustilago* (Pers.) Roussel species due to their interactions with viruses (Schmitt and Breing, 2002; Marquina et al., 2007). Killer isolates secrete proteinous toxins (mostly cell wall degrading enzymes) against sensitive cells of the same or closely related species, while the producing cells themselves are immune. These types of killer isolates could be beneficial in medicine, agriculture and industry (Schmitt and Breing, 2002).

We have also seen that three-part interaction provide thermal tolerance by the plant (Marquez et al., 2007). Another example is the A78 virus of *Aspergillus fumigatus* Fresen causing mild hypervirulence on *Galleria_mellonella* (L., 1758) (Greater wax moth) (Ozkan and Coutts, 2015). Likewise, TmPV1 associated with *T. marneffei* caused hypervirulence on *T. marneffei* in the mouse host (Lau et al., 2018).

Liu et al. (2022) reported that mycovirus *Stemphylium lycopersici* alternavirus 1 (SlAV1) from a necrotrophic plant pathogen (*Stemphylium lycopersici)* that causes altered colony pigmentation and hypovirulence by specifically interfering host biosynthesis of Altersolanol A, a polyketide phytotoxin.

Li et al. (2019) reported that most *Fusarium* mycoviruses establish latent infections, but some mycoviruses such as *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) cause hypovirulence. Khan et al. (2023) emphasized that among members of the genus *Sclerotinia*, a huge number of mycoviruses have been identified; some of them have a hypovirulent effect on the fitness of their fungal hosts.

Zhou et al. (2021) revealed that mycoviruses have been associated with plant adaptation to extreme environments, conferring heat tolerance to plants that contain fungal endophytes. They reported that endophytic fungi, can confer fitness to the host plants. It is unclear whether biological factors can modulate the parasitic and mutualistic traits of a fungus. Kotta-Loizou (2021) affirmed that in fungus-mycovirus-environmental interactions, the environment and both abiotic and biotic factors play crucial roles in whether and how mycovirus mediated phenotypes are manifest.

Connor (2021) reported that soybean leaf-associated gemycircularvirus-1 (SlaGemV-1) is capable of inducing hypovirulence in the highly pathogenic fungus *Sclerotinia sclerotiorum* as does the hypovirus 1 (CHV1) controlling *C. parasitica* in chestnut in Europe. It is an excellent model organism for studying hypovirulence in fungi (Anagnostakis et al., 1998; Liu and Milgroom, 2007).

Kirchman (2018) pointed out that viruses infecting fungi do not appear to lyse their host. The use of mycovirus can open many avenues for handling waste and decomposition, or terminating some life processes. For instance grazers completely oxidize the organic content of their host into carbon dioxide and inorganic nutrients. A third mode of employing viruses may theoretically be to facilitate the exchange of genetic material from one host to another. Most of these processes have been relatively poorly studied (Pearson et al., 2009).

Hypovirulence may be induced in hosts by mycoviruses via RNA silencing, alteration of genetic expression, and disruption of the transcriptome that can result in phenotypic changes like reduction in growth or changes in pigmentation (Nuss, 2005). Alterations of miRNAs expressions using viral suppressors of RNA silencing (VSRs) occurs by applying papain-like protease p29 (Segers et al., 2006) and potyvirus HC-Pro (Maia et al., 1996). Also, *C. parasitica* when infected by the hypovirulence-inducing mycovirus undergoes RNA silencing thereby affecting the MAPK cascade and G-protein signaling. Moreover, direct disruption of the fungal transcriptome may occur (Nuss, 2005).

Proof of the ability of a mycovirus being able to control a pathogen in the field is either scarse or unavailable (Griffin 1986, MacDonald et al. 1991) but mycoviruses have been shown to be able to control fungi in modified environments (MacDonald et al., 1991; Milgroom et al., 2004).

Two major forms of defense signaling include: systemic acquire resistance (SAR) and induced systemic resistance (ISR). (Vidhyasekaran, 2015). Another theoritical approach usable to increase a plant resistance against pathogenic infection is resistance priming like that involved in SsHADV-1 allowing *S. sclerotiorum* to induce priming in plants. ‘Priming is the process of inoculating plants, often the seeds, with beneficial microorganisms to improve nutrient use efficiency and to potentially improve resistance to pathogens’ (Rakshit et al., 2015). Actually, Qu et al. (2020) demonstrated that SsHADV-1-infected, hypovirulent *S. sclerotiorum* is reprogrammed to act as a beneficial, bio-priming mycorrhiza in rapeseed due to *Sclerotinia* Fuckel stem rot reduction and improved yield. Mycoviruses have been shown to be involved in all forms of interactions (e.g. mutualism) with fungi hosts. In the future, mycoviruses may be required for manipulating micro-ecosystems within plants, humans, animals and so on. They are simple enough for direct insertion and removal of genes here and there if the right equipment is available. However, pathogenic mycoviruses have been reported and they can severely ravage host populations especially domesticated mushrooms e.g. la France disease on *Agaricus bisporus*. Thus, mycoviruses have to be controlled in fungus-fungus, fungus-plant, fungus-animal systems, etc.

Ruiz-Padilla et al. (2021) propounded that products based on microorganisms (including mycoviruses senso lato) can be used in biocontrol strategies alternative to chemical control. Keçeli (2017) reported that the use of mycoviruses in the treatment of invasive fungal infections in humans has not been suggested yet. Xie and Jiang (2014) suggested that fungal vegetative incompatibility is likely to be the limiting factor in the widescale utilization of mycoviruses to control crop diseases.

4 CONCLUSION

Past, present and future trends in mycovirus research are of interest to humans. They can reveal the prospects of mycoviruses in agriculture and the environment in terms of pathogen control and amelioration of the environment. Use of mycoviruse to induce hypovirulence in fungi host isolates has shown great potentials e.g. using the A78 virus of *Aspergillus fumigatus,* TmPV1 on *T. marneffei*, soybean leaf-associated gemycircularvirus-1 (SlaGemV-1) in *Sclerotinia sclerotiorum,* the hypovirus 1 (CHV1) in *Cryphonectria parasitica.* Hypovirulence may be induced in fungi hosts by mycoviruses via RNA silencing, alteration of genetic expression, and disruption of the transcriptome which can result in phenotypic changes like reduction in growth or changes in pigmentation. Moreover, direct disruption of the fungal transcriptome may occur. Another approach to increase a plant’s resistance against pathogenic infection is resistance priming that may be required for manipulating micro-ecosystems within the plants. However, pathogenic mycoviruses have been reported and they can severely ravage host populations especially domesticated mushrooms

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