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AWARD

Molecular biological studies on viruses infecting filamentous fungi and showing neo-lifestyles

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Introduction

Viruses are omnipresent across life forms and have a diverse impact on their hosts. Advances in bioinformatics have led to the identification of many previously unknown viruses, emphasizing the importance of understanding their novel lifestyles. Mycoviruses, i.e., viruses that infect fungi, are useful for the understanding of viral evolution and virus-eukaryote interactions as well as for controlling fungal diseases (Sato and Suzuki 2023). This review summarizes novel viral characteristics and virus-virus and virus-host interactions that have been found through the studies of viruses in phytopathogenic filamentous fungi.

Capsidless multi-segmented viruses

Understanding of the molecular entities of viruses is essential for their discovery and study. Typically, viruses enclose their genomes within protein shells known as capsids. RNA viruses with many (around ten) genomic segments, such as those in the order *Reovirales* that accommodates double-stranded RNA (dsRNA) viruses from various eukaryotic hosts, encapsidate their entire genome within a single capsid (Sato et al. 2018; Varsani et al. 2018). In contrast, hadaka virus 1 (HadV1), discovered in *Fusarium oxysporum*, the causal agent of Fusarium wilt, possesses an eleven-segmented RNA genome that does not encode any putative capsid proteins (Sato et al. 2020b). Unlike conventional encapsidated viruses, HadV1 cannot be precipitated by ultracentrifugation. Moreover, HadV1 RNAs in host crude extracts are susceptible to RNase, further distinguishing them from encapsidated viruses. Among known viruses, HadV1 is phylogenetically closest to members of the family *Polymycoviridae*, which comprises unusual multi-segmented dsRNA viruses proposed to exist either as semi-capsidless colloidal forms or as filamentously encapsidated particles (Kotta-Loizou et al. 2022). However, polymycoviruses are precipitable by ultracentrifugation and resistant to RNase in host crude extracts, underscoring the distinctive nature of HadV1 (Khan et al. 2021; Sato et al. 2020a, b). These findings led to the establishment of the new virus family *Hadakaviridae* in the phylum *Pisuviricota* to accommodate HadV1 (Sato et al. 2023c). A closely related capsidless virus, later identified in the anthracnose pathogen *Colletotrichum fructicola*, is associated with the formation of giant vesicles in the host hyphae, which are hypothesized to encapsulate the viral RNAs (Fu et al. 2022). Additional potentially capsidless, multi-segmented RNA viruses have been identified in the family *Splipalmiviridae* in the phylum *Lenarviricota* (Sabanadzovic et al. 2025). These viruses are particularly unusual in that they encode the RNA-dependent RNA polymerase, the hallmark of RNA viruses, in a split form across two genomic segments (Chiba et al. 2021; Sutela et al. 2020). Members of this group have been detected in various filamentous fungi, although the host range of each virus appears to be limited (Sato et al. 2022b). The occurrence of distinct multi-segmented capsidless viruses in independent viral lineages suggests a distinctive pattern of viral evolution in their filamentous fungal hosts.

Virus-virus-host three-way relationships

Multiple viruses can coinfect a single host, yet their interactions and effects on hosts remain poorly understood. A novel type of virus–virus interaction, termed "yadokari" (room borrower) and "yadonushi" (room owner), describes

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a relationship in which capsidless single-stranded (ssRNA) viruses depend on encapsidated dsRNA viruses for their replication, hypothetically by utilizing the heterocapsids as replication sites (Zhang et al. 2016). An increasing number of viruses capable of such interactions are being found. As representative cases, ssRNA viruses in the family *Yadokariviridae* are known to collectively partner with dsRNA viruses in multiple families within the order *Ghabrivirales*, while each yadokarivirus selectively interacts with specific dsRNA viruses at the species level (Sato et al. 2022a, 2023a). The outcomes of such coinfections on hosts vary, ranging from negative to positive (Sato et al. 2022a). In an intriguing case, a yadokarivirus reduces the accumulation of its partner virus that is virulent to the host fungus *Rosellinia necatrix*, the causal agent of white root rot, and thereby rescues the host from growth defects. Remarkably, yadokari–yadonushi interactions can also occur in heterologous experimental hosts (Sato et al. 2023b). Moreover, a *Tombusviridae*-related capsidless ssRNA virus is heteroencapsidated by a *Ghabrivirales* dsRNA virus in a plant host, indicating that similar interactions may extend beyond fungi (Antunes et al. 2016). Together, these findings point to the broader prevalence of yadokari–yadonushi interactions across different viruses and hosts, highlighting the need to further elucidate their molecular mechanisms as well as their biological and ecological consequences.

A novel antiviral mechanism related to RNA interference

Comparative immunology sheds light on how antiviral mechanisms evolve and function across different organisms, thereby facilitating a mutual understanding of these processes in diverse virus-host systems (tenOever 2016). RNA interference (RNAi or RNA silencing) serves as an antiviral mechanism in a wide range of eukaryotes (Guo et al. 2019). In this process, Dicer dices viral dsRNA structures and generates small interfering RNA (siRNA) duplexes. Argonaute then binds to the siRNA and cleaves complementary viral ssRNA or inhibits its translation. Consequently, Argonaute has long been considered the effector of antiviral RNAi. However, a Dicer-dependent, Argonaute-independent antiviral mechanism has been demonstrated in the chestnut blight fungus *Cryphonectria parasitica* (Sato et al. 2024). This fungus upregulates *Dicer* gene expression upon viral infection, and the dicing of viral dsRNA is sufficient to block certain dsRNA viruses even in Argonaute-null mutants. The contribution of Argonaute to viral suppression varies depending on the virus, highlighting the need for a better understanding of the mechanisms underlying these differential outcomes. Although the theoretical possibility of an Argonaute-independent, dicing-based antiviral defense has been speculated (Pumplin and Voinnet 2013), it has not yet been experimentally demonstrated in animals or plants, which require Argonaute for development, making complete knockout experiments technically difficult. In contrast, Argonaute-null mutants in *C. parasitica* grow normally in the absence of viruses, enabling researchers to address this question directly. This underscores the significance of fungi as model organisms for investigating eukaryotic antiviral mechanisms.

Conclusion

Studies of viruses infecting phytopathogenic filamentous fungi have revealed unconventional viral features and interactions that challenge and expand our current understanding of virology. In plant pathology, these findings are valuable not only for employing mycoviruses to control fungal diseases but also for providing insights into virus–host interactions in other systems, such as those between viruses and plants. As experimentally tractable and evolutionarily informative models, fungal viruses offer unique opportunities to rethink what viruses are, how they behave within communities, and how hosts respond to them.

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Declarations

Conflict of interest The author declares no conflict of interest.

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