

Biodiversity beyond the visible – molecular actors in apple cultivation

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Abstract

*Biodiversity in fruit production is typically associated with varietal diversity, beneficial organisms, soil and landscape structures. For example, surveys of traditional apple orchards in Germany have documented 3,625 species. However, microscopic to molecular levels – the microbiome, virome, and subviral elements such as viroids – have received far less attention. These “molecular actors” can influence the health, yield, and quality of apple orchards, often without causing visible symptoms. Investigations into the apple virome reveal a wide diversity not only of pathogenic but also of latent viruses and viroids, whose actual relevance for fruit quality and resilience remains largely unclear. For instance, the apple hammerhead viroid (AHVd) is widespread in German orchards, yet no consistent correlation with yield or quality has been established so far. Looking beyond apples reveals potential: in citrus production, rootstocks are deliberately inoculated with naturally occurring citrus dwarfing viroid (CDVd) to control tree size – with positive effects on pruning effort and harvest efficiency. Bacteriophages are being explored as a biological control strategy against *Erwinia amylovora* (fire blight), and transposons are known as natural drivers of growth-related mutations. This raises the question: must all viral elements in apple production be considered threats – or can deeper insight into molecular biodiversity unlock new opportunities for enhancing stress tolerance, growth regulation, or sensory traits?*

Keywords: apple virome, genetic ecology, plant virus, viroid, transposons, phage

Introduction – from macro- to micro-biodiversity

Traditional apple orchards are biodiversity hotspots hosting over 3,600 documented species (Henle et al., 2024). Yet biodiversity extends beyond visible organisms to include the apple microbiome—diverse microbial communities comprising pathogens, beneficial organisms, and biocontrol agents (Abdelfattah et al., 2021; 2022). At the molecular scale, viromes, viroids, and transposons act as “molecular actors” shaping plant growth, fruit quality, and resilience. Recent findings challenge traditional host-pathogen boundaries: plant viruses and viroids have been detected in fungal hosts (Tian et al., 2022; Xia et al., 2025), while phages show promise as biocontrol agents against *Erwinia amylovora*, the causal agent of fire blight (Biosca et al., 2024). Transposable elements drive phenotypic shifts, including columnar growth and fruit coloration (Otto et al., 2013; Zhang et al., 2019), and contribute to adaptive traits during domestication (Wang et al., 2023). These molecular entities form a dynamic network connecting plant, pathogen, and symbiont across kingdoms—a hidden genetic ecosystem shaped by co-evolution and competition. Understanding these interactions may unlock new strategies for managing apple health through microbial and viral biodiversity. This paper reviews molecular biodiversity in apple—from microbiome to viromes, viroids, and transposons—examining whether molecular actors traditionally viewed as threats might offer opportunities for resilient organic production.

The apple microbiome – invisible communities

Apple trees harbor a remarkably complex microbiome across leaves, flowers, fruits, and roots, composed of hundreds of bacterial and fungal genera. Global surveys identified

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several thousand species across the phyllosphere, carposphere, and rhizosphere (Abdelfattah et al., 2021). The authors identified a global core microbiome for the apple cultivar 'Royal Gala', including bacterial genera *Sphingomonas* and *Methylobacterium*, and fungal genera *Aureobasidium*, *Cladosporium*, and *Alternaria* (Abdelfattah et al., 2021). The ecological roles of these microorganisms extend far beyond pathogenesis. *Sphingomonas* and *Methylobacterium* are known for their plant growth-promoting and stress-protective effects, including phytohormone modulation, detoxification of reactive oxygen species, and colonization resistance against pathogens (Droby & Wisniewski, 2018). *Aureobasidium pullulans*, a common epiphyte on apple fruit surfaces and member of the core microbiome, is already used in commercial postharvest biocontrol formulations (e.g., BoniProtect) due to its antagonistic activity against major pathogens such as fire blight and others (Raynaldo et al., 2024; Droby & Wisniewski, 2018). Several apple-associated microbes, including *Methylobacterium* and *Cladosporium*, are also recognized as human-beneficial, contributing to a balanced dietary microbiota.

Microbiome composition reflects orchard management intensity. A recent comparison of organic and integrated production systems showed that organic orchards host a different functionally active microbiome, characterized by stronger activation of plant defense-related pathways and distinct community structures (Bartuv et al., 2023). Wild apple species such as *Malus sieversii* and *M. orientalis* harbor even higher microbial diversity than cultivated apples, indicating that domestication and management have narrowed microbial associations, potentially reducing resilience (Abdelfattah et al., 2022). Collectively, these findings highlight the apple microbiome as a dynamic, invisible layer of biodiversity—linking plant health, disease suppression, and even aspects of human well-being.

The apple virome – latent infections and hidden interactions

The apple virome comprises a variety of RNA and DNA viruses, often coexisting with viroids and subviral elements. While many infections remain latent, their ecological and agronomic effects are increasingly recognized. Virome surveys from Iran, the Czech Republic, and India revealed that most apple trees harbor complex virus communities, frequently involving apple stem grooving capillovirus (ASGV), apple chlorotic leaf spot virus (ACLSV), and apple stem pitting virus (ASPV) (Hamedi et al., 2025; Manzour et al., 2025; Khan et al., 2024). However, apple green crinkle-associated virus (AGCaV) was most prevalent in Iran, while apple necrotic mosaic virus (ApNMV) was found mainly in China and Japan, highlighting regional variation in viral composition (Xing et al., 2018). These viruses are among the most persistent infections in *Malus domestica*, often asymptotically in commercial cultivars.

ACLSV is globally distributed and transmitted by grafting. Most infections remain symptomless (latent), complicating eradication (Manzoor et al., 2023; Wunsch et al., 2024). Another important pathogen is apple mosaic virus (ApMV), which can cause mosaic symptoms and leaf deformations with negative effects on tree growth, fruit yield, and quality (Manzoor et al., 2023; Grimová et al., 2016). Next-generation sequencing has uncovered additional viruses including apple luteovirus 1 (ALV-1), apple rubbery wood virus 1 and 2 (ARWV1, ARWV2), and citrus concave gum-associated virus (CCGaV) (Wunsch et al., 2024; Hamedi et al., 2025; Manzour et al., 2025; Seinsche et al., 2026). ARWV1 and ARWV2 have been associated with apple rubbery wood disease, though ARWV1 also occurs in asymptomatic trees (Seinsche et al., 2026; Manzour et al., 2025). Mixed infections are prevalent, with most Iranian and Czech samples harboring multiple viral agents simultaneously (Hamedi et al., 2025; Manzour et al., 2025).

Four viroids are currently known to infect apple, apple scar skin viroid (ASSVd) and the closely related apple dimple fruit viroid (ADFVd), as well as the globally distributed viroids

hop stunt viroid (HSVd) and apple hammerhead viroid (AHVd). For ASSVd, no severe symptoms or major outbreaks have been reported in Europe, although the viroid has been detected in several countries, including Denmark, France, Greece, Italy, Poland, and the United Kingdom (CABI Compendium 6086). AHVd has emerged as the globally most widespread viroid in apple orchards. For example, a recent survey in Germany found it in 78 % of all tested samples (Zikeli et al., 2025). Despite its ubiquity, symptom expression is inconsistent, with some cultivars showing leaf blotches or growth reduction. Small-RNA sequencing identified abundant viroid-derived small RNAs, suggesting regulatory roles and interactions with host RNA-silencing machinery (Zikeli et al., 2025). Although these viroids cannot yet be tightly linked to specific symptoms, evidence from other pathosystems suggests that symptomless infections can still modify host metabolism. For instance, hop latent viroid (HLVd) in *Humulus lupulus* modifies the plant's metabolic profile and product quality without macroscopic symptoms (Patzak et al., 2021).

Mixed viral infections are common in apple, with up to eight viruses and one viroid detected per tree (Xiao et al., 2022). These consortia can interact synergistically or antagonistically, modifying disease outcomes and symptom expression depending on viral combinations and environmental context (Moreno & López-Moya, 2020). The apple virome thus represents a multilayered network blurring the boundary between pathogen and symbiont.

In regulatory and certification contexts, a limited subset of these viruses is routinely monitored. According to the EPPO standard PM 4/27(1) and its implementation in Germany, virus-free mother plants are routinely required to be test negative for ACLSV, ASGV, ASPV, ApMV. Additionally, the ASSVd and apple proliferation phytoplasma are included in the broader EPPO testing framework. Although not part of the apple virome in a strict sense, '*Candidatus Phytoplasma mali*' (the causal agent of apple proliferation) is often included in certification schemes together with major viruses and viroids (EPPO PM 4/27). It represents another invisible molecular threat in apple production, transmitted through grafting and psyllid vectors, and capable of drastically altering tree morphology, vigor, and fruit quality.

Lessons from other crops – viroids as regulators

The case of citrus dwarfing viroid (CDVd) illustrates that viroids can act as functional regulators rather than pathogens. In California, CDVd has been intentionally introduced into rootstock–scion combinations of sweet orange grafted on trifoliolate orange to induce a controlled dwarfing phenotype. Infected trees exhibit half the canopy volume and about 20% shorter shoot growth, compared to CDVd-free trees. Further, the CDVd-infected trees maintain normal fruit yield per cultivation area at the same quality (Lavagi-Craddock et al., 2022). Transcriptome analyses revealed that CDVd infection reprograms host gene expression in stems and roots, including altered regulation of transcription factors such as MYB13 and MADS-box genes associated with meristem function and stress responses. Importantly, no activation of defense pathways was detected, supporting the view that CDVd behaves as a transmissible small nuclear RNA, rather than a pathogen, since this RNA modifies tree physiology without causing disease quality (Lavagi-Craddock et al., 2022). This example shows that subviral RNAs can function as natural growth regulators in perennial fruit systems, offering an intriguing biological alternative to chemical growth control. Importantly, this approach does not involve genetic engineering but utilizes naturally occurring viroids already present in citrus.

Molecular allies: phages and mycoviruses

Another class of viruses relevant for the genetic ecology of apple are mycoviruses. These are typically highly host-specific viruses infecting fungi that can reshape plant–pathogen

relationships. Infection of *Alternaria alternata* f. sp. *mali* with two RNA mycoviruses reduced virulence and suppressed production of the phytotoxin alternariol (Li et al., 2022). Similarly, co-infection of *Valsa mali*, the causal agent of apple canker, with *Cryphonectria hypovirus 1* or *Mycoreovirus 1* markedly decreased fungal aggressiveness (Yang et al., 2021). In apple replant disease soils, new potentially hypovirulence inducing mycoviruses have been detected in *Rugonectria rugulosa*, a root-associated endophyte and occasional pathogen, revealing the hidden viral diversity within the apple rhizosphere (Pielhop et al., 2022).

Cross-kingdom interactions between viruses, viroids and fungi have been reported, though the underlying mechanisms remain poorly understood. Recent studies detected ASSVd RNA in several fungal species isolated from infected apple trees (Tian et al., 2022). The results of the study further showed that ASSVd-positive fungi exhibit altered phenotypes—including reduced virulence in *Epicoccum nigrum* (Tian et al., 2022), which may point to more research for viral biocontrol agents. Similarly, ASGV was detected in *Fusarium solani* isolates from virus-infected apple orchards (Xia et al., 2025). While these findings suggest potential cross-kingdom transmission, direct evidence of viral replication in fungal hosts and the biological significance of such associations require further investigation.

Phages also deserve consideration, as these viruses infect bacteria—either beneficial or pathogenic—and can therefore influence both the microbiome and plant–pathogen relationships. Phages targeting *Erwinia amylovora* have gained renewed attention as biological alternatives to antibiotics and copper compounds. Biosca et al. (2024) isolated and characterized lytic bacteriophages of the genus *Kolesnikvirus* from Mediterranean environments and demonstrated their efficacy against *E. amylovora* in vitro and in detached fruit assays. Phage cocktails applied preventively reduced disease severity by up to 86% under controlled conditions. However, several challenges remain, including bacterial resistance development, sensitivity to environmental stressors, and the need for field validation. These phages represent a promising avenue for biocontrol, but their practical application in integrated or organic production systems will require further optimization and regulatory approval.

Transposons – genetic biodiversity within the apple genome

Transposable elements represent endogenous components of biodiversity, shaping genome structure and function in all eukaryotes. In apples, their activation has produced several agronomically relevant mutations. A striking example is the *Wjczik* mutation of the apple cultivar ‘McIntosh’, in which the insertion of a Ty3/Gypsy-like long terminal repeat (LTR) retrotransposon on chromosome 10 is associated with the columnar phenotype (Otto et al., 2013). The retrotransposon insertion led to ectopic expression changes in nearby genes, including a 2-oxoglutarate-Fe(II) oxygenase (the *Co* locus), resulting in the compact, spur-type tree architecture later exploited in breeding (Dougherty et al., 2020; Otto et al., 2013). A second, well-characterized case involves a retrotransposon insertion upstream of the transcription factor gene *MdMYB1*, a core regulator of anthocyanin biosynthesis. The presence of this LTR element correlates with red fruit skin coloration by enhancing *MdMYB1* expression (Zhang et al., 2019). Together, these findings demonstrate that transposon activity can directly influence key traits such as tree architecture and fruit quality.

Recent genome-scale analyses further highlight the pervasive role of transposable elements in the apple genome. A pan-genome of thirteen *Malus* accessions revealed more than 317,000 structural variants and over 20,000 copy number variations, many associated with gene expression changes and fruit quality traits (Wang et al., 2023). Another pangenom assembly confirmed that segmental duplications and insertions contributed to the expansion of resistance gene analogs during domestication, partly driven by transposon-mediated

rearrangements (Su et al., 2024). Across 26 *Malus* accessions, genome size correlated strongly with transposable-element content, suggesting that TEs serve as major contributors to genome expansion (Chang et al., 2025). Interestingly, evidence from other crops suggests that the boundaries between transposons and viral elements may be more fluid than previously assumed. In soybean, fragments of cucumber mosaic virus RNA were found integrated into the host genome, possibly facilitated by transposon-associated integrase activity (da Fonseca et al., 2016). Such findings challenge the traditional separation of endogenous and exogenous genetic elements and support the view of a shared genetic ecology among transposons, viruses, and their hosts. Altogether, these studies position transposons as central drivers of genetic biodiversity within the apple genome. By mediating insertions, duplications, and regulatory innovations, they generate a continuous source of variation that underlies morphological, biochemical, and adaptive diversity in *Malus domestica* and its wild relatives.

Discussion

Although most molecular actors appear latent or beneficial, their stability depends on environmental and management context. Rising temperatures may alter virus-host equilibria, turning latent infections symptomatic. Heat and drought may also activate endogenous transposons, altering gene expression under field conditions.

Because many viruses and viroids are symptomless, infected material can be unknowingly propagated through rootstocks or scions. Even certified "virus-free" plants are tested for only a few viruses, leaving newly described or latent agents undetected. This hidden transmission risk increases when old cultivars or wild genotypes are reintroduced for diversification. Mixed infections and molecular crosstalk between viruses, viroids, and transposable elements may amplify stress responses or symptom expression, yet such multilayered interactions remain unexplored and could explain differences in resilience.

However, this hidden molecular biodiversity may also provide opportunities for ecological production. Naturally occurring viroids used for citrus stunting demonstrate that subviral RNAs can act as biological growth regulators without genetic modification, suggesting potential for size control or stress modulation in apple using indigenous viral elements. Phages offer promising alternatives to antibiotics and copper-based treatments for fire blight control, combining host specificity with environmental compatibility. Transposons provide a natural source of genetic innovation; their utilization in breeding could generate novel architectures, pigmentation patterns, or adaptive traits.

Apple production faces challenges from latent viruses and viroids, yet molecular biodiversity may offer new opportunities. Should growers focus primarily on virus eradication, or could deliberate inclusion of certain viral or subviral elements enhance resilience and reduce external inputs? Integrating these invisible molecular actors into the broader concept of biodiversity could foster more resilient and ecologically balanced apple production systems, though this requires long-term monitoring and deeper integration of molecular diagnostics, stress physiology, and ecological management.

References

- Abdelfattah, A., Freilich, S., Bartuv, R., Zhimo, V. Y., Kumar, A., Biasi, A., et al. (2021). Global analysis of the apple fruit microbiome: are all apples the same? *Environmental Microbiology*, 23(10), 6038–6055. <https://doi.org/10.1111/1462-2920.15469>
- Abdelfattah, A., Tack, A. J. M., Wasserman, B., Liu, J., Berg, G., Norelli, J., et al. (2022). Evidence for host–microbiome co-evolution in apple. *New Phytologist*, 234(6), 2088–2100. <https://doi.org/10.1111/nph.17820>

- Bartuv, R., Berihu, M., Medina, S., Salim, S., Feygenberg, O., Faigenboim-Doron, A., et al. (2023). Functional analysis of the apple fruit microbiome based on shotgun metagenomic sequencing of conventional and organic orchard samples. *Environmental Microbiology*, 25(9), 1728–1746. <https://doi.org/10.1111/1462-2920.16353>
- Biosca, E. G., Delgado Santander, R., Morán, F., Figàs-Segura, À., Vázquez, R., Català-Senent, J. F., & Álvarez, B. (2024). First European *Erwinia amylovora* Lytic Bacteriophage Cocktails Effective in the Host: Characterization and Prospects for Fire Blight Biocontrol. *Biology*, 13(3), 176. <https://doi.org/10.3390/biology13030176>
- Chang, C., Xie, Z., Zhang, S., Shao, D., Ma, X., Tong, L., et al. (2025). Pangenome-wide characterization of the TCP gene family and its potential role in regulating adventitious shoot regeneration in apple. *Agriculture Communications*, 3(3), 100101. <https://doi.org/10.1016/j.agrcom.2025.100101>
- da Fonseca, G. C., de Oliveira, L. F. V., de Moraes, G. L., Abdelnor, R. V., Nepomuceno, A. L., Waterhouse, P. M., et al. (2016). Unusual RNA plant virus integration in the soybean genome leads to the production of small RNAs. *Plant Science*, 246, 62–69. <https://doi.org/10.1016/j.plantsci.2016.01.011>
- Dougherty, L., Bai, T., Brown, S., & Xu, K. (2020). Exploring DNA Variant Segregation Types Enables Mapping Loci for Recessive Phenotypic Suppression of Columnar Growth in Apple. *Frontiers in Plant Science*, 11(June). <https://doi.org/10.3389/fpls.2020.00692>
- Droby, S., & Wisniewski, M. (2018). The fruit microbiome: A new frontier for postharvest biological control. *Postharvest Biology and Technology*, 140, 107–112. <https://doi.org/10.1016/j.postharvbio.2018.03.004>
- Grimová, L., Winkowska, L., Konrady, M., & Ryšánek, P. (2016). Apple mosaic virus. *Phytopathologia Mediterranea*, 55(1), 1–19. https://doi.org/10.14601/PHYTOPATHOL_MEDITERR-16295
- Hamed, A., Rakhshandehroo, F., Safarnejad, M. R., Jouzani, G. S., Ben Slimen, A., & Elbeaino, T. (2025). Comprehensive Virome Profiling of Apple Mosaic Disease-Affected Trees in Iran Using RT-PCR and Next-Generation Sequencing. *Viruses*, 17(7), 979. <https://doi.org/10.3390/v17070979>
- Henle, K., Hüttner, M.-L., Kasperidus, H. D., Krämer, J., Rösler, M., Bartelt, S., et al. (2024). Streuobstbestände in Deutschland. Naturschutzfachliche Bedeutung, Bestandssituation und Handlungsempfehlungen. *BfN-Schriften*, 679, 1–156. <https://doi.org/10.19217/skr679>
- Khan, Z. A., Sharma, S. K., Gupta, N., Diksha, D., Thapa, P., Shimray, M. Y., et al. (2024). Assessing the de novo assemblers: a metaviromic study of apple and first report of citrus concave gum-associated virus, apple rubbery wood virus 1 and 2 infecting apple in India. *BMC Genomics*, 25(1), 1057. <https://doi.org/10.1186/s12864-024-10968-x>
- Lavagi-Craddock, I., Dang, T., Comstock, S., Osman, F., Bodaghi, S., & Vidalakis, G. (2022). Transcriptome Analysis of Citrus Dwarfing Viroid Induced Dwarfing Phenotype of Sweet Orange on Trifoliate Orange Rootstock. *Microorganisms*, 10(6), 1144. <https://doi.org/10.3390/microorganisms10061144>
- Li, B., Cao, Y., Ji, Z., Zhang, J., Meng, X., Dai, P., et al. (2022). Coinfection of Two Mycoviruses Confers Hypovirulence and Reduces the Production of Mycotoxin Alternariol in *Alternaria alternata* f. sp. mali. *Frontiers in Microbiology*, 13(June), 1–14. <https://doi.org/10.3389/fmicb.2022.910712>
- Manzoor, S., Nabi, S. U., Baranwal, V. K., Verma, M. K., Parveen, S., Rather, T. R., et al. (2023). Overview on century progress in research on mosaic disease of apple (*Malus domestica* Borkh) incited by apple mosaic virus/apple necrotic mosaic virus. *Virology*, 587(July), 109846. <https://doi.org/10.1016/j.virol.2023.109846>
- Manzoor, S., Nabi, S. U., Ayaz, A., Rasool, B., Sharma, S. K., Chesti, M. H., et al. (2025). Unveiling viral threats to temperate pome fruits: characterization, transmission, and sustainable management strategies. *Frontiers in Microbiology*, 16(March), 1–13. <https://doi.org/10.3389/fmicb.2025.1560720>

- Moreno, A. B., & López-Moya, J. J. (2020). When viruses play team sports: Mixed infections in plants. *Phytopathology*, 110(1), 29–48. <https://doi.org/10.1094/PHYTO-07-19-0250-FI>
- Otto, D., Petersen, R., Brauksiepe, B., Braun, P., & Schmidt, E. R. (2013). The columnar mutation of apple (*Malus x domestica*) is associated with an integration of a Gypsy-like retrotransposon. *Molecular Breeding*, 33(4), 863–880. <https://doi.org/10.1007/s11032-013-0001-3>
- Patzak, J., Henychová, A., Krofta, K., Svoboda, P., & Malířová, I. (2021). The Influence of Hop Latent Viroid (HLVd) Infection on Gene Expression and Secondary Metabolite Contents in Hop (*Humulus lupulus* L.) Glandular Trichomes. *Plants*, 10(11), 2297. <https://doi.org/10.3390/plants10112297>
- Pielhop, T. P., Popp, C., Knierim, D., Margaria, P., & Maiß, E. (2022). Three new mycoviruses identified in the apple replant disease (ARD)-associated fungus *Rugonectria rugulosa*. *Virus Genes*, 58(5), 423–435. <https://doi.org/10.1007/s11262-022-01924-6>
- Raynaldo, F. A., Xu, Y., Yolandani, Wang, Q., Wu, B., & Li, D. (2024). Biological control and other alternatives to chemical fungicides in controlling postharvest disease of fruits caused by *Alternaria alternata* and *Botrytis cinerea*. *Food Innovation and Advances*, 3(2), 135–143. <https://doi.org/10.48130/fia-0024-0014>
- Seinsche, C., Berwarth, C., Brodbeck, M., Zikeli, K., Vondran, A., Kleemann, L., et al. (2026). Development of novel detection primers and screening for apple rubbery wood virus 1 and 2 in Germany. *Journal of Virological Methods*, 339(May 2025). <https://doi.org/10.1016/j.jviromet.2025.115241>
- Su, Y., Yang, X., Wang, Y., Li, J., Long, Q., Cao, S., et al. (2024). Phased telomere-to-telomere reference genome and pangenome reveal an expansion of resistance genes during apple domestication. *Plant Physiology*, 195(4), 2799–2814. <https://doi.org/10.1093/plphys/kiae258>
- Tian, M., Wei, S., Bian, R., Luo, J., Khan, H. A., Tai, H., et al. (2022). Natural Cross-Kingdom Spread of Apple Scar Skin Viroid from Apple Trees to Fungi. *Cells*, 11(22), 3686. <https://doi.org/10.3390/cells11223686>
- Wang, T., Duan, S., Xu, C., Wang, Y., Zhang, X., Xu, X., et al. (2023). Pan-genome analysis of 13 *Malus* accessions reveals structural and sequence variations associated with fruit traits. *Nature Communications*, 14(1). <https://doi.org/10.1038/s41467-023-43270-7>
- Wunsch, A., Hoff, B., Sazo, M. M., van Zoeren, J., Lamour, K. H., Hurtado-Gonzales, O. P., & Fuchs, M. (2024). Viruses of Apple Are Seedborne but Likely Not Vertically Transmitted. *Viruses*, 16(1), 95. <https://doi.org/10.3390/v16010095>
- Xia, Y., Li, B., Wu, X., Han, Z., Zhang, K., Hao, P., et al. (2025). Transmission of apple stem grooving virus (*Capillovirus mali*) to apple from the soil-borne fungus *Fusarium solani*. *BMC Plant Biology*, 25(1), 1226. <https://doi.org/10.1186/s12870-025-07188-0>
- Xiao, H., Hao, W., Storoschuk, G., MacDonald, J. L., & Sanfaçon, H. (2022). Characterizing the Virome of Apple Orchards Affected by Rapid Decline in the Okanagan and Similkameen Valleys of British Columbia (Canada). *Pathogens*, 11(11). <https://doi.org/10.3390/pathogens11111231>
- Xing, F., Robe, B. L., Zhang, Z., Wang, H. Q., & Li, S. F. (2018). Genomic analysis, sequence diversity, and occurrence of apple necrotic mosaic virus, a novel ilarvirus associated with mosaic disease of apple trees in china. *Plant Disease*, 102(9), 1841–1847. <https://doi.org/10.1094/PDIS-10-17-1580-RE>
- Yang, S., Dai, R., Salaipeth, L., Huang, L., Liu, J., Andika, I. B., & Sun, L. (2021). Infection of Two Heterologous Mycoviruses Reduces the Virulence of *Valsa mali*, a Fungal Agent of Apple Valsa Canker Disease. *Frontiers in Microbiology*, 12(May), 1–14. <https://doi.org/10.3389/fmicb.2021.659210>
- Zhang, L., Hu, J., Han, X., Li, J., Gao, Y., Richards, C. M., et al. (2019). A high-quality apple genome assembly reveals the association of a retrotransposon and red fruit colour. *Nature Communications*, 10(1), 1–13. <https://doi.org/10.1038/s41467-019-09518-x>
- Zikeli, K., Berwarth, C., Born, U., Leible, T., Jelkmann, W., & Hagemann, M. H. (2025). Prevalence, genetic diversity, and molecular detection of the apple hammerhead viroid in Germany. *Frontiers in Microbiology*, 16. <https://doi.org/10.3389/fmicb.2025.1592572>