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Aphids as Vectors of Plant Viruses: Mechanisms of Transmission and Host Interaction

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Abstract This study systematically reviews the mechanisms by which aphids act as vectors for plant viruses and their interactions with host plants. By synthesizing recent findings on the molecular and ecological aspects of aphid-transmitted plant viruses, this study explores the significant roles of aphid biology, morphology, and endosymbionts in virus transmission. Plant viruses can manipulate host plant physiology to enhance transmission efficiency, with changes including virus-induced impacts on host metabolism and gene expression, thereby altering aphid behavior and increasing transmission effectiveness. This study also reveals that aphids exhibit complex behavioral and physiological adaptations in virus transmission. Understanding the interactions between aphids, viruses, and host plants is crucial for developing effective management strategies to mitigate the global agricultural impact of aphid-transmitted plant viruses.

Keywords Aphids; Plant viruses; Virus transmission; Host interaction; Pest management

1 Introduction

Aphids are among the most destructive insect pests affecting agricultural crops globally. These small, sap-sucking insects are notorious for their ability to cause direct damage to plants through their feeding behavior, which depletes essential nutrients and weakens plant structures. Aphids possess piercing-sucking mouthparts that facilitate their feeding on phloem sap, leading to significant yield losses in various crops, including potatoes, citrus, and hemp (Xu and Gray, 2020; Pitt et al., 2022). Additionally, aphids are vectors for numerous plant viruses, which further exacerbate their impact on agriculture. For instance, the green peach aphid (*Myzus persicae*) and the potato aphid (*Macrosiphum euphorbiae*) are known to transmit several economically important viruses to potato crops, resulting in severe yield reductions and loss of tuber quality.

Understanding the mechanisms of virus transmission by aphids is crucial for developing effective management strategies to mitigate their impact on agriculture. Aphids transmit plant viruses through various modes, including non-persistent, semi-persistent, and persistent (circulative and non-circulative) transmission (Jayasinghe et al., 2021). The interaction between aphids, plant viruses, and host plants is complex and involves multiple factors, including aphid biology, virus characteristics, and plant responses (Gadhave et al., 2020; Ray and Casteel, 2022). For example, the transmission efficiency of viruses like Potato Virus Y (PVY) can be influenced by the feeding behavior of aphids, which is affected by both the virus and the host plant suitability (Pitt et al., 2022). Moreover, plant viruses can manipulate host plant physiology to enhance their transmission by aphid vectors, as seen in the case of Turnip Yellows Virus (TuYV), which alters the plant's nutritive content and defense mechanisms to benefit both the virus and the aphid vector (Krieger et al., 2023).

Recent studies have also highlighted the role of insect-specific viruses and symbiotic bacteria in influencing aphid behavior and virus transmission. For instance, the *Aphis citricidus* Picorna Virus (AcPV) affects the stylet penetration activity of the brown citrus aphid, facilitating its transmission (An et al., 2023). Similarly, the presence of symbiotic bacteria like *Serratia symbiotica* in aphids can aid in suppressing plant defenses, thereby enhancing aphid feeding and virus transmission (Skaljac et al., 2019). These findings underscore the importance of a holistic understanding of the interactions between aphids, plant viruses, and host plants to devise sustainable pest management strategies.

This study integrates current knowledge on the mechanisms by which aphids transmit viruses and their interactions with host plants, examining the latest advancements in this field, including the role of aphid biology and morphology in virus transmission, the impact of viral infection on aphid feeding behavior, and the molecular interactions among plant viruses, aphids, and host plants, to provide a comprehensive understanding of factors influencing aphid-mediated virus transmission, with the goal of identifying potential targets for developing sustainable management strategies to mitigate the impact of aphid-transmitted viruses on global agriculture.

2 Mechanisms of Virus Transmission by Aphids

2.1 Non-persistent transmission

Non-persistent transmission involves viruses that are acquired and transmitted by aphids within a short period, typically during brief probing of the plant epidermis. These viruses do not circulate within the aphid's body but are retained in the stylets. For instance, the Papaya Ringspot Virus (PRSV) is transmitted in a non-persistent manner by the melon aphid (*Aphis gossypii*). PRSV-infected plants enhance the fitness and feeding behavior of *A. gossypii*, likely through nutrient enrichment, which in turn facilitates virus transmission (Gadhave et al., 2019). Potyviruses, the largest group of plant-infecting RNA viruses, are also predominantly transmitted non-persistently by aphids, influencing aphid behavior and host plant biochemistry to enhance transmission efficiency (Gadhave et al., 2020).

2.2 Semi-persistent transmission

In semi-persistent transmission, viruses are retained in the foregut or salivary glands of the aphid but do not circulate within the insect's body. These viruses can be retained for a longer period compared to non-persistent viruses. The transmission process involves specific interactions between the virus capsid and retention sites in the vector. For example, Non-Circulative, Semi-Persistent (NCSP) viruses have evolved mechanisms to bind to specific sites in the aphid's foregut, facilitating prolonged retention and transmission. This mode of transmission is influenced by the vector's feeding behavior and the plant's response to virus infection, which can alter vector attraction and feeding patterns (Zhou et al., 2018).

2.3 Persistent transmission

Persistent transmission involves viruses that circulate within the aphid's body, moving from the gut to the hemolymph and eventually to the salivary glands. These viruses can be retained for the lifetime of the aphid. For instance, the Turnip Yellows Virus (TuYV) is transmitted persistently by aphids in a circulative, non-propagative manner. TuYV infection alters the host plant's metabolic composition, reducing defense responses and enhancing the plant's suitability as a feeding site, which promotes higher transmission efficiency (Chesnais et al., 2022; Krieger et al., 2023). Persistent viruses manipulate plant traits to create a more favorable environment for aphid feeding and virus transmission over extended periods (Shi et al., 2021).

2.4 Circulative and non-circulative pathways

Viruses transmitted by aphids can follow either circulative or non-circulative pathways. In the circulative pathway, viruses enter the aphid's gut, circulate through the hemolymph, and reach the salivary glands, as seen with TuYV (Krieger et al., 2023). In contrast, non-circulative viruses, such as potyviruses, are retained in the stylets or foregut and do not enter the hemolymph. The mode of transmission (circulative or non-circulative) significantly influences the virus-vector-plant interactions, with circulative viruses often inducing more profound changes in plant physiology to enhance vector attraction and feeding (Chesnais et al., 2022).

2.5 Factors influencing transmission efficiency

Several factors influence the efficiency of virus transmission by aphids, including the virus's ability to manipulate host plant traits, the vector's feeding behavior, and the presence of endosymbionts. For example, the presence of the endosymbiont *Buchnera aphidicola* in aphids can modulate the volatile profile of host plants, affecting aphid feeding preferences and virus transmission dynamics (Shi et al., 2021). Additionally, virus-induced changes in plant defense responses and nutrient profiles can either enhance or deter aphid feeding, thereby influencing transmission efficiency (Gadhave et al., 2019; Shi et al., 2021; Krieger et al., 2023). Understanding these complex interactions is crucial for developing effective strategies to manage aphid-transmitted plant viruses.

3 Host Interaction and Virus Acquisition

3.1 Aphid feeding behavior and stylet penetration

Aphid feeding behavior and stylet penetration are critical for the transmission of plant viruses. The Electrical Penetration Graph (EPG) technique has been utilized to study the feeding behavior of aphids, revealing that virus infection can alter aphid feeding patterns. For instance, cannabis aphids (*Phorodon cannabis*) demonstrated different feeding behaviors on hemp and potato, which influenced the transmission efficiency of Potato Virus Y (PVY) (Pitt et al., 2022). Additionally, the presence of insect-specific viruses, such as *Aphis citricidus* Picorna Virus (AcPV), can affect the stylet penetration activity of aphids, thereby facilitating virus transmission (An et al., 2023). These findings highlight the complex interactions between aphids, their feeding behavior, and virus transmission.

3.2 Virus-vector interactions at the cellular level

At the cellular level, virus-vector interactions involve intricate mechanisms that facilitate virus acquisition and transmission (Figure 1) (Catto et al., 2022). Plant viruses can manipulate host plant physiology to enhance their transmission by vectors. For example, the Turnip Yellows Virus (TuYV) alters the metabolic composition of infected plants, which benefits both the aphid vector and the virus transmission (Krieger et al., 2023). Furthermore, the presence of endosymbionts like *Buchnera aphidicola* in aphids can modulate virus transmission by affecting the volatile profile of host plants, leading to changes in aphid feeding preferences (Shi et al., 2021). These cellular-level interactions underscore the co-evolutionary dynamics between plant viruses, aphids, and host plants.

3.3 Host plant responses to aphid-virus infections

Host plants exhibit various responses to aphid-virus infections, which can influence virus transmission. Transcriptome profiling of *Arabidopsis thaliana* and *Camelina sativa* infected with different viruses revealed virus- and host-specific gene expression changes that impact aphid behavior and virus transmission (Chesnais et al., 2022). Additionally, the presence of plant lectins can reduce virus transmission by interfering with the virus-aphid interaction. For instance, feeding aphids with Pisum Sativum Lectin (PSL) significantly reduced the transmission efficiency of barley yellow dwarf virus and potato virus Y (Francis et al., 2020). These host plant responses play a crucial role in the overall dynamics of aphid-virus interactions.

3.4 Evolutionary adaptations of aphids in virus transmission

Aphids have evolved various adaptations to enhance their efficiency as virus vectors. These adaptations include changes in feeding behavior, stylet penetration, and interactions with host plants and endosymbionts. For example, the melon aphid (*Aphis gossypii*) shows increased performance and arrestment on Papaya Ringspot Virus (PRSV)-infected plants due to enhanced nutrient profiles, which in turn promotes virus transmission (Gadhave et al., 2020). Additionally, the co-evolution of aphids and plant viruses has led to the development of mutualistic interactions, where both the virus and the vector benefit from the interaction (Ray and Casteel, 2022). These evolutionary adaptations highlight the complex and dynamic nature of aphid-virus interactions.

4 Molecular Mechanisms Underlying Virus Transmission

4.1 Role of viral proteins in facilitating aphid-mediated transmission

Viral proteins play a crucial role in facilitating the transmission of plant viruses by aphids. For instance, the interaction between viral proteins and aphid proteins is essential for the efficient transmission of viruses like the Potato Leafroll Virus (PLRV). Studies have identified several aphid proteins that interact with PLRV, including an orthologue of the human innate immunity protein complement Component 1 Q Subcomponent-Binding Protein (C1QBP). This protein partially co-localizes with PLRV in the cytoplasmic puncta and along the periphery of aphid gut epithelial cells, indicating its role in the acquisition and transmission efficiency of PLRV by *Myzus persicae* (DeBlasio et al., 2021). Additionally, the identification of cuticular proteins such as Stylin-01 in aphid mouthparts has provided insights into the mechanisms of noncirculative virus transmission. Stylin-01 has been shown to be involved in the transmission of the Cauliflower Mosaic Virus (CaMV) by binding to the virus in the acrostyle of aphid stylets (Webster et al., 2018).

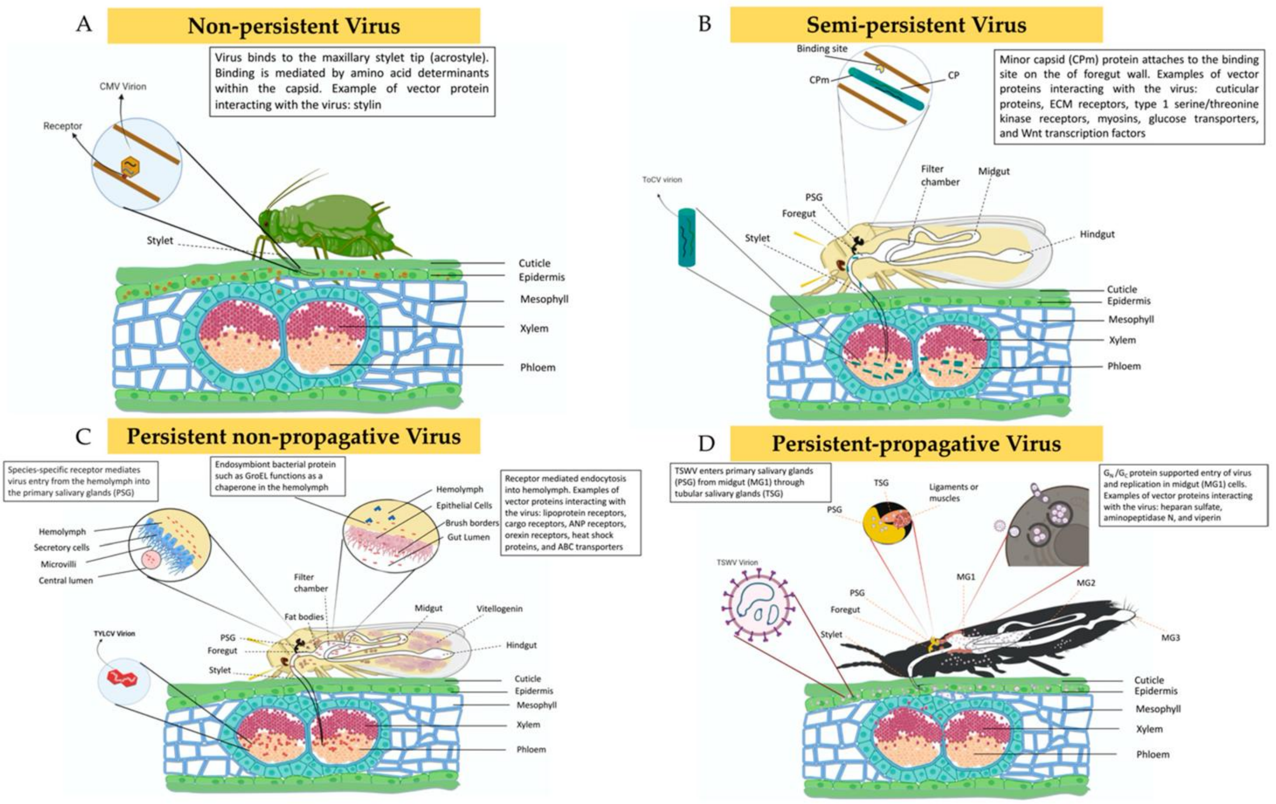

Figure 1 Schematic diagram explaining the interactions between plant viruses and their vectors with respect to different transmission modes viz., non-persistent, semi-persistent, persistent non-propagative, and persistent-propagative (Adopted from Catto et al., 2022)
Image caption: (A) Non-persistent viruses, such as Cucumber Mosaic Virus (CMV), are acquired by aphids from the epidermal cells of infected plants and retained at the tip of its stylet (acrostyle) at the distal end of the common (food/salivary) duct. (B) Semi-persistent viruses, such as Tomato Chlorosis Virus (ToCV), are phloem-limited in infected plants, and the virus attaches to the binding site at the vector's foregut with the help of the minor Capsid Protein (CPm). (C) Persistent non-propagative viruses, such as Tomato Yellow Leaf Curl Virus (TYLCV), are also phloem-limited and are retained in the midgut upon acquisition. Through receptor-mediated endocytosis, the virus traverses the midgut barrier into hemolymph where the endosymbiont protein GroEL interacts with the virion. The virus from the hemolymph reaches primary salivary glands mediated again via species-specific receptors. (D) Thrips acquire persistent propagative viruses, such as Tomato Spotted Wilt Virus (TSWV), from epidermal cells of infected plants. Gn/Gc protein supports virus entry into midgut cells, where replication of the virus occurs. The virus TSWV enters Primary Salivary Glands (PSG) from MG1 through Tubular Salivary Glands (TSG) (Adopted from Catto et al., 2022)

4.2 Aphid genomic and transcriptomic insights into virus transmission

Genomic and transcriptomic analyses have revealed significant insights into the molecular interactions between aphids and plant viruses. For example, transcriptome profiling of *Arabidopsis thaliana* and *Camelina sativa* plants infected with Turnip Yellows Virus (TuYV) or CaMV and infested with *Myzus persicae* aphids has shown virus- and host-specific differences in gene expression patterns. These differences are linked to the mode of virus transmission and the severity of symptoms, which in turn affect aphid behavior and fecundity (Chesnais et al., 2022). Furthermore, a review of transcriptional responses in various insect vectors, including aphids, has cataloged differential gene expression related to virus reception, cell entry, tissue tropism, and vector immune responses. This understanding can aid in identifying candidate genes for targeted management approaches using RNAi or CRISPR editing (Catto et al., 2022).

4.3 Virus-induced alterations in aphid behavior and physiology

Plant viruses can induce significant alterations in aphid behavior and physiology to enhance their transmission. For instance, the Turnip Yellows Virus (TuYV) has been shown to alter the metabolic composition of infected plants, which in turn benefits the aphid vector and increases virus transmission efficiency. The virus infection alleviates gene deregulations induced by aphids in non-infected plants, leading to changes in the plant's nutritive content and defense reactions (Krieger et al., 2023). Similarly, the Papaya Ringspot Virus (PRSV) has been found to enhance the fitness of its vector, the melon aphid (*Aphis gossypii*), by increasing the concentrations of essential amino acids and soluble carbohydrates in the host plant. This results in increased aphid arrestment and long-term feeding on PRSV-infected plants, thereby promoting virus transmission (Gadhave et al., 2019). Additionally, the interaction between plant viruses and aphid vectors often involves mutualistic relationships where both the virus and the vector benefit from the interaction. Viral and vector effectors target conserved mechanisms of plant immunity, manipulating host physiology to facilitate successful colonization and transmission (Ray and Casteel, 2022).

5 Case Study

5.1 Specific case of aphid-mediated virus transmission in crop plants

Aphids are notorious vectors of plant viruses, significantly impacting crop production worldwide. One notable example is the transmission of the Turnip Yellows Virus (TuYV) by aphids in *Arabidopsis thaliana*. This virus is transmitted in a circulative and non-propagative manner, meaning the virus circulates within the aphid but does not replicate within it. Research has shown that TuYV infection can alleviate the gene deregulations induced by aphid infestation, thereby promoting virus transmission. The virus alters the plant's metabolic composition, making it more conducive for aphid feeding and increasing transmission efficiency (Figure 2) (Krieger et al., 2023). Another significant case involves the transmission of Potato Virus Y (PVY) by the cannabis aphid (*Phorodon cannabis*). This aphid species has been shown to efficiently transmit PVY to both hemp and potato plants, with varying transmission rates depending on the host plant (Pitt et al., 2022).

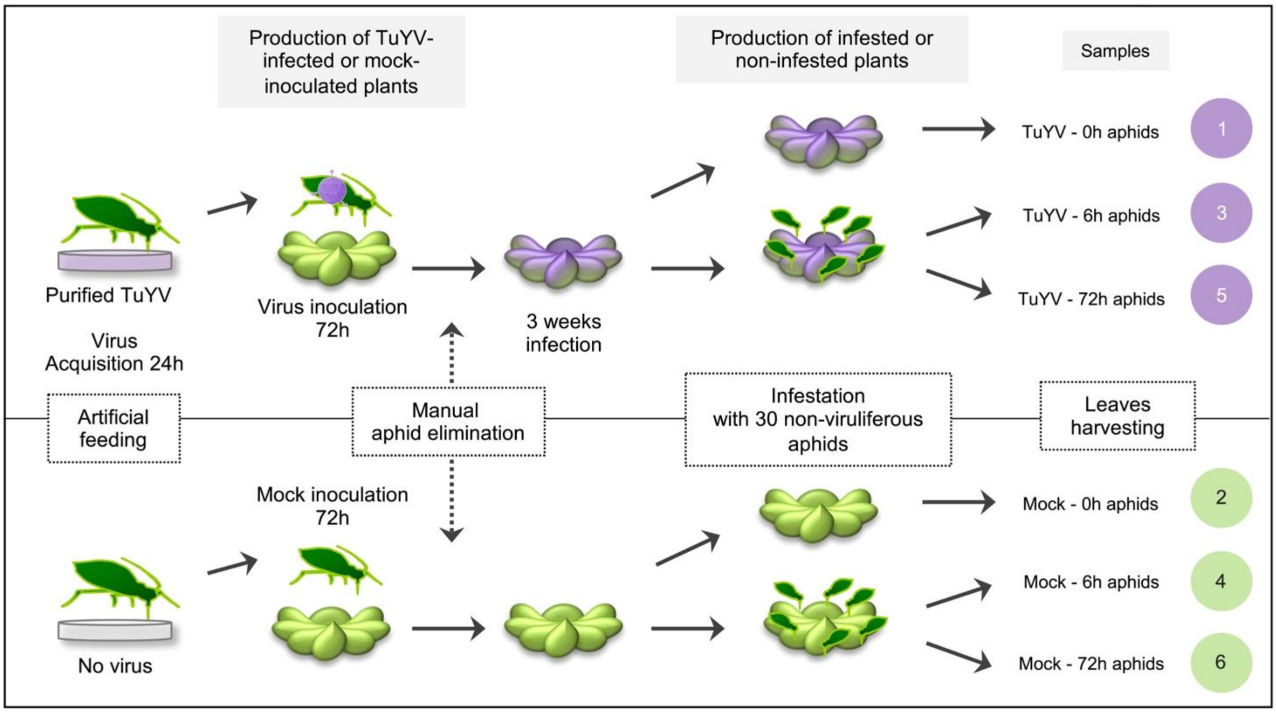

Figure 2 Experimental set-up for the high-throughput transcriptomic and metabolomic analyses (Adopted from Krieger et al., 2023)
Image caption: Arabidopsis plants were inoculated with Turnip Yellows Virus (TuYV)-viruliferous (upper panel) or nonviruliferous (lower panel) *Myzus persicae*aphids. After 3 weeks, the two batches of plants were infested with 30 nonviruliferous aphids for 6 or 72 h before harvesting (samples 3 to 4 and 5 to 6, respectively). Plants that were not infested with aphids were similarly processed (samples 1 and 2) (Adopted from Krieger et al., 2023)

5.2 Analysis of virus spread dynamics in a real-world scenario

The dynamics of virus spread in real-world agricultural settings are complex and influenced by multiple factors, including aphid behavior, plant-virus interactions, and environmental conditions. For instance, the spread of non-persistent viruses like PVY is heavily influenced by the feeding behavior of aphids. Studies using the Electrical Penetration Graph (EPG) technique have shown that viruliferous aphids (those carrying the virus) exhibit different feeding behaviors compared to non-viruliferous aphids, which can affect virus transmission rates. Viruliferous aphids tend to spend less time ingesting phloem, potentially leading to increased dispersal and virus spread (Pitt et al., 2022). Additionally, epidemiological models have demonstrated that agronomic practices such as fertilization, irrigation, and pesticide application can significantly impact the spread of non-persistent viruses. For example, fertilization and irrigation can either reduce or increase virus spread depending on whether the interference between resident and transient aphids is direct or indirect (Zaffaroni et al., 2021).

5.3 Impact on crop yield and agricultural practices

The impact of plant viruses on crop yields can be severe, leading to significant reductions in both quantity and quality of the produce (Zhan, 2024). The impact of aphid-mediated virus transmission on crop yield and agricultural practices is profound. Viruses like TuYV and PVY can cause significant yield losses, necessitating the development of effective management strategies. For instance, the presence of TuYV in *Arabidopsis thaliana* has been shown to alter the plant's nutritive content and defense mechanisms, making it more susceptible to aphid infestation and virus transmission (Krieger et al., 2023). Similarly, the efficient transmission of PVY by cannabis aphids can lead to substantial yield losses in both hemp and potato crops (Pitt et al., 2022). To mitigate these impacts, various strategies have been proposed, including the use of plant lectins to reduce virus transmission efficiency. Feeding aphids with specific plant lectins has been shown to significantly reduce the transmission of viruses like Barley Yellow Dwarf Virus and Potato Virus Y, offering a potential alternative approach for crop protection (Francis et al., 2020). Additionally, understanding the interactions between aphids, viruses, and plant hosts at the molecular level can inform the development of targeted pest management strategies, such as the use of chemical inhibitors to disrupt key protein-protein interactions involved in virus transmission (DeBlasio et al., 2021).

6 Strategies for Managing Aphid-Mediated Virus Transmission

6.1 Biological control methods

Biological control methods involve the use of natural predators, parasitoids, and pathogens to manage aphid populations and reduce virus transmission. One promising approach is the use of entomopathogenic fungi, such as *Beauveria bassiana*, which has shown effectiveness in reducing virus transmission rates. For instance, endophytic colonization of melon plants with *B. bassiana* significantly reduced the transmission rates of Cucumber Mosaic Virus (CMV) and Cucurbit Aphid-Borne Yellows Virus (CABYV) by 21.9% and 24.4%, respectively (González-Mas et al., 2019). Additionally, the manipulation of aphid endosymbionts, such as *Buchnera aphidicola*, can alter aphid behavior and reduce virus transmission. For example, CMV infection reduces *B. aphidicola* abundance in aphids, leading to a shift in feeding preference from infected to healthy plants, thereby potentially reducing the spread of the virus (Shi et al., 2021).

6.2 Chemical control and integrated pest management (IPM)

Chemical control methods, including the use of insecticides, are commonly employed to manage aphid populations. However, the indiscriminate use of pesticides can lead to resistance development and non-target effects. Integrated Pest Management (IPM) strategies combine chemical control with other methods to achieve sustainable pest management. For example, the application of pesticides can be optimized by understanding the interactions between resident and transient aphids. An epidemiological model showed that pesticide application could counterintuitively increase the spread of non-persistent viruses if not properly managed, highlighting the importance of integrating ecological principles into pest management strategies (Zaffaroni et al., 2021). Additionally, the use of selective insecticides that target specific aphid species while preserving natural enemies can enhance the effectiveness of IPM programs.

6.3 Breeding virus-resistant plant varieties

Breeding virus-resistant plant varieties is a long-term strategy to manage aphid-mediated virus transmission. Resistant varieties can reduce the incidence of virus infections and limit the spread of viruses by aphids. Advances in understanding the molecular mechanisms of plant-virus-vector interactions have facilitated the development of resistant varieties. For instance, the identification of plant transcription factors and protein degradation pathways targeted by virus and vector effectors can inform breeding programs aimed at enhancing plant resistance (Ray and Casteel, 2022). Additionally, the manipulation of plant nutrient profiles to deter aphid feeding and reduce virus transmission has shown promise. For example, PRSV-infected plants exhibited increased concentrations of essential amino acids and soluble carbohydrates, which enhanced the fitness of the melon aphid, suggesting that altering plant nutrient profiles could be a potential strategy for breeding resistant varieties (Gadhave et al., 2019).

6.4 Future directions in aphid management for virus control

Future research in aphid management for virus control should focus on a multidisciplinary approach that integrates biological, chemical, and genetic strategies. Understanding the complex interactions between aphids, viruses, and host plants at the molecular level can inform the development of targeted control methods. For instance, the use of effector-mediated interactions to manipulate host plant physiology and enhance resistance to both aphids and viruses is a promising area of research (Ray and Casteel, 2022). Additionally, the development of ecological models that incorporate environmental factors and microbial communities can improve our understanding of disease dynamics and inform the deployment of microbiome-targeted pest management tactics (Enders and Hefley, 2023). Finally, exploring the potential of novel biotechnological approaches, such as RNA interference (RNAi) and gene editing, to disrupt virus transmission pathways in aphids could provide new avenues for sustainable pest management.

7 Concluding Remarks

Aphids are significant vectors of plant viruses, and their interactions with both the viruses they transmit and the host plants they infest are complex and multifaceted. Recent research has highlighted the role of effector proteins in mediating these interactions, with both viruses and aphids using effectors to manipulate host plant physiology to their advantage. Studies have shown that plant viruses can alter the host plant's metabolic and gene expression profiles to facilitate their transmission by aphids. For instance, the Turnip Yellows Virus (TuYV) can alleviate aphid-induced stress responses in *Arabidopsis thaliana*, thereby enhancing its own transmission. Additionally, the transmission efficiency of potyviruses, the largest group of plant-infecting RNA viruses, is influenced by various factors including aphid behavior and host plant biochemistry. Aphid biology and morphology also play crucial roles in virus transmission, with different transmission modes (persistent, circulative, non-circulative) being affected by these factors. Furthermore, the presence of endosymbionts in aphids can modulate virus transmission by altering the volatile profiles of host plants, thereby influencing aphid feeding behavior.

Understanding the mechanisms of aphid-mediated virus transmission has significant implications for crop protection and virus control. The ability of viruses to manipulate host plant responses to benefit their transmission suggests that targeting these molecular interactions could be a viable strategy for controlling virus spread. For example, the use of plant lectins to interfere with virus transmission by aphids has shown promise, as lectins can bind to viral glycoproteins and reduce transmission efficiency. Additionally, manipulating the nutrient profile of host plants to make them less favorable for aphid vectors could reduce virus transmission rates. The role of endosymbionts in modulating virus transmission also opens up new avenues for pest management, such as targeting symbionts to disrupt the transmission process. Overall, integrating these insights into pest management strategies could lead to more effective and sustainable approaches to controlling aphid-transmitted plant viruses.

Future research should focus on further elucidating the molecular mechanisms underlying aphid-virus-host plant interactions. This includes identifying specific effector proteins involved in these interactions and understanding their roles in manipulating host plant physiology. Additionally, more studies are needed to explore the impact of different environmental factors on virus transmission dynamics, particularly in the context of climate change. The role of microbial communities within aphids and their influence on virus transmission also warrants further investigation, as this could lead to novel microbiome-targeted pest management strategies. Moreover, the development of multi-omics approaches to study these complex interactions at a systems level could provide deeper insights into the co-evolutionary dynamics between aphids, viruses, and host plants. Finally, translating these findings into practical applications for crop protection will require interdisciplinary collaboration between molecular biologists, entomologists, plant pathologists, and agronomists.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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