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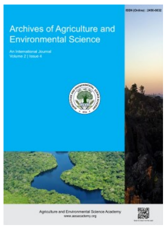

REVIEW ARTICLE

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An ideal model of plant-vector-phytopathogen interaction and the management of the vector

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ABSTRACT

Maize (*Zea mays* L.) is a vital cereal crop worldwide, crucial for global food security and various industrial applications. Its cultivation faces significant challenges from a diverse array of insect pests and pathogens, notably including the maize leaf aphid (*Rhopalosiphum maidis*) and the maize dwarf mosaic virus (MDMV). This paper explores the intricate interactions among maize, its insect vectors, and MDMV, emphasizing the urgent need for a deeper understanding to develop sustainable management strategies. Maize exhibits vast genetic diversity and is cultivated across diverse environments, making it susceptible to a range of pests and diseases. The transmission of MDMV by aphids, particularly *R. maidis*, poses a significant threat to maize production globally. The complex tripartite interaction between maize, aphids, and MDMV serves as an ideal model system for studying plant-insect-phytopathogen interactions. Understanding the components of this interaction is critical for developing effective management strategies. Despite significant research efforts, there remains a knowledge gap in the molecular mechanisms underlying vector-borne diseases. Further research on the molecular level is essential for identifying specific targets for genetic pest control and disrupting pathogen transmission by insect vectors. Developing countries, in particular, require intensified research efforts to address the growing challenges to food security and agricultural sustainability. Thus, unraveling the complexities of plant-insect-phytopathogen interactions is essential for devising effective strategies to combat vector-borne diseases and sustain global food systems. Enhanced scientific research, especially in developing regions, is crucial for addressing these challenges and ensuring food security for future generations.

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INTRODUCTION

Maize (*Zea mays* L.) stands as a cornerstone in global agriculture, crucial for ensuring food security worldwide (Miedaner & Juroszek, 2021). It is the third-largest crop grown in developing countries, a major staple crop in sub-Saharan Africa (Abate *et al.*, 2017), and a major component of food and feed in Asia (Witt *et al.*, 2006). However, beyond its significance as a staple food and feed, maize plays a pivotal role in various industrial applications, notably as a source for fuel ethanol production, in the early twenties, about 41.2% of total maize production was used for fuel ethanol production, in the U.S., and the rate has been increasing ever since (Klopfenstein *et al.*, 2013). Maize possesses great diversity in genetics and is grown in a wide range of environments, from the equator to about 50° north latitudes and 42° south latitudes and as high as 3800 meters above sea level; this wide range of variation in maize cultivation makes it a favorable host for a large population of insect pests and diseases. The cultivation of maize spans diverse environments, presenting a rich genetic diversity that also attracts a plethora of insect pests and diseases, among which homopterans emerge as notable vectors for transmitting numerous viral diseases. Among them are the group of insects that not only feed on maize but also play a significant role in disease transmission.

These insect groups are the carrier (vectors) for the disease agents and hinder plants' growth and development by sucking the sap; called homopterans. These homopterans mediate more than 400 viral disease transmissions in plants (Hogenhout *et al*., 2008). Aphid (Order: Homoptera, Family: Aphididae) alone transmits more than 200 species of persistent or non-persistent plant viruses (Moury *et al*., 2007). Likewise, aphids are one of the serious pests of maize that vector the transmission of viral diseases. One of the serious viral diseases of maize, maize dwarf mosaic (MDM) disease, known since the 1960s and reported in Africa, the United States, Asia, and Europe (Kannan *et al*., 2018), is widely transmitted by corn/maize leaf aphid (*Rhopalosiphum maidis*) in a non-persistent manner (Ortega *et al*., 1987; Hogenhout *et al*., 2008). The interplay among maize, its insect vectors, and MDMV offers an ideal model for understanding plant-insect-phytopathogen interactions, crucial for devising effective management strategies. The Maize Dwarf Mosaic Virus (MDMV) is transmitted by aphid vectors through a short acquisition access period (AAP) of 10–30 seconds. Prolonging acquisition time can increase virus retention in aphid stylets, enhancing transmission efficiency. Virus particles attach to aphid appendages via the capsid protein (CP) and helper component proteinase (HC-Pro), acting as a "molecular bridge" for transmission. A specific amino acid sequence (DAG) near the CP N-terminus is crucial for virus transmission. HC-Pro facilitates this interaction, as the N-terminus alone may not effectively interact with aphid stylets. Understanding these mechanisms informs targeted control strategies against MDMV. Despite considerable advancements, over 700 vector-borne plant diseases threaten global food security, underscoring the urgent need for enhanced understanding of plant-insect interactions (Fletcher & Wayadanda, 2002). The interaction of maize, maize leaf aphid, and maize dwarf mosaic virus is an ideal model to illustrate a typical plant, insect vector, and phytopathogen interaction. The long-studied phytopathogen and its hosts suggest a model that can unravel the possibilities of plant-insect interaction. Studying the interactions between insect vectors, phytopathogens, and their shared plant hosts fundamentally elucidates the clues necessary for developing sustainable and novel control strategies to mitigate losses caused by vector-borne plant diseases. Henceforth, there is a need to augment our knowledge of the plant-insect interaction (Pincebourde *et al*., 2017).

One of the immediate sustainable management approaches to control the pest population below the economic threshold level is Integrated Pest Management (IPM). The principle behind the IPM is to integrate biological control, modification of cultural practices, habitat manipulation, and use of resistant varieties (Flint, 2012). It assures long-term prevention of pest and their damage. Pesticides are applied only after monitoring indications of their need based on the established guidelines or principles (Peshin & Zhang, 2014). IPM is a decision-based approach that involves optimizing the pest population below the economic threshold by the coordinated use of multiple tactics in an economically and environmentally sound manner (Ehler, 2006). Integrated Pest Management (IPM) encompasses a comprehensive approach to pest management, incorporating physical, cultural, biological, and chemical control methods. Regular monitoring aids in timely interventions, while physical tactics such as traps and removal of infected plants disrupt pest populations. Biological control involves introducing natural enemies like parasitic wasps and predators, while cultural practices like weed management and balanced fertilizer use mitigate pest pressure. Chemical controls are employed sparingly and strategically to minimize environmental impact, with preference given to safer options like insecticidal soaps and oils for managing maize leaf aphids. The management of maize leaf aphids can be achieved effectively if IPM is practiced (Williamson, 2019).

Components of plant-insect (vector)-phytopathogen interaction

Maize: Maize (*Zea mays*), also known as corn, is a member of the grass family Poaceae (Perera & Weerasinghe, 2014). Maize originated in Mexico (Ranum et al., 2014) and disseminated further North and South of its center of origin. It is cultivated widely throughout the world and has the highest production among all the cereals. Considered one of the fastest-growing cash crops in the world and becoming the largest component of the global coarse grain trade, it is a preferred staple food for 120 -140 million poor farm families, 900 million poor, and about one-third of all malnourished children globally (Murdia *et al*., 2016). Maize plays a significant role in human nutrition; it contains 60–68% starch, 7–15% protein, rich in amino acids and minerals (phosphorus and potassium), it is extensively used for animal feed and is also utilized for biofuel production (Serna-Saldivar & Carrillo, 2018). For over a century, maize has been established as a genetic model of the monocotyledonous plant, which makes it an ideal model for studying plant-insect (vector)-phytopathogen interaction (Yang *et al*., 2019). There are seven known vector-borne diseases of maize; among them five are viral: Maize dwarf mosaic virus potyvirus A, Maize dwarf mosaic virus potyvirus B, Maize rayado fino marafivirus, Maize mosaic nucleorhabdovirus, and Maize stripe tenuivirus, while the other two are bacterial: corn stunt spiroplasma and maize bushy stunt phytoplasma (Tsai & Falk, 2022). Interestingly, 25 species of aphids (including *Rhopalosiphum maidis*, *Myzus persicae*, *Rhopalosiphum padi*, *Rhopalosiphum poae*, *Brevicoryne brassicae*, and *Rhopalosiphum fitchii*) are known to vector MDMV non-persistently in maize (Kunkel, 1921). Among them, the maize leaf aphid (*Rhopalosiphum maidis*) is one of the major insect vectors (Kannan *et al*., 2018). The viral pathogens transmitted by *R. maidis* have been reported in all maize-growing regions and have caused damage, ranging from 38.9% to 98.8%, with an average loss of 71.7% (Yoon-Sup, 2003). There is limited scientific information available regarding the targets and mechanisms of resistance in maize against *R. maidis* infections. Therefore, it is important to understand the components of the maize dwarf mosaic disease. Studies focusing on the mechanisms of maize pathogen transmission could provide major clues on the interactions of plant-insect vector-phytopathogen interaction that might aid in disrupting transmission and offering sustainable control strategies.

Maize leaf aphid: The maize leaf aphid (*Rhopalosiphum maidis*) is soft-bodied (Family: Aphididae) belonging to the order Homoptera. Having piercing-sucking mouthparts, they are highly efficient plant viral vectors and have the potential to transmit both persistent and non-persistent viruses (Moury *et al.*, 2007). These aphids are light to dark green and have two darker patches at the base of each cornicle (siphunculi) (Parrish, 1967). Adults have an oblong-shaped body and antennae (typically darker in color) that extend to about one-third of the body length and the legs; they can grow up to 2 mm long. Nymphs are similar to adults; however, smaller in size and always wingless, whereas adults may be winged or wingless (Wildermuth & Walter, 1932). The maize leaf aphids have approximately 9 generations per year. Female aphids give birth to young ones, called nymphs, unlike other insects that lay eggs (Dixon, 1977). The nymphs resemble adults but are smaller and sexually immature. Mostly, these aphids are wingless; however, as their population increases, some of them may develop delicate and transparent wings to fly to uninfested plants to begin a new colony (Valenzuela & Hoffmann, 2015). These aphids can survive and reproduce optimally during autumn and spring, and development rates are favored when daily maximum temperatures reach 20° to 26° C. During this time, the aphids' population may reach several generations (Valenzuela & Hoffmann, 2015). Moreover, aphids can be found all year round, often persisting on a range of grasses or self-sown cereals (during summer and early autumn); winged aphids fly into crops from grass weeds, pastures, or other cereal crops, and start to build up colonies within the crop (Straub & Boothroyd, 1980).

Maize Dwarf Mosaic Virus (MDMV)

MDMV belongs to the family Potyviridae; there are 8 genera under the family; *Potyvirus*, *Tritimovirus*, *Brambyvirus*, *Rymovirus*, *Ipomovirus*, *Bymovirus*, *Macluravirus*, *and Poacevirus* (Matthews, 1989). MDMV belongs to the genus *Potyvirus*. The virus is rod-shaped and flexuous having a length of 750 nm and a diameter of 12–15 nm (Tosic *et al.*, 1990). It is a holoparasite and requires a vector or host to reproduce and survive (Cao *et al.*, 2011). Since the infected plants take up to 15 days to exhibit the symptoms, to eliminate the dependence on symptoms for identification, both molecular and serological methods have been developed to diagnose MDM-diseased plants (Trzmiel, 2008). The distribution of viral particles was observed generally in the cytoplasm and less frequently in plasmodesmata (Chauhan, 1985). The in vitro MDMV lasts 1–2 days at room temperature, while it lasts for 3–5 days at 0–4^0 C (Baumgarten, 1981). The minimum temperature required to inactivate MDMV completely is 54^0–58^0C (Deng *et al.*, 2008). Similar to other potyviruses, MDMV is also a positive-stranded RNA (Gell *et al.*, 2015). Having a covalently bounded viral-genome-linked protein and VPg at its 50 end as well as a poly (A) tail attached to its 30 end, the MDMV genome is ~9500 base pairs in length (Gell *et al.*, 2015). From a single open reading frame (ORF), a large 338 kDa polyprotein is translated (Kong & Steinbiss, 1998), which is cleaved proteolytically by three self-coded proteinases to obtain 10 final proteins (P1, HC-Pro, P3, 6K1, CI, 6K2, NIa-VPg, NIa-Pro, NIb, and CP) (Gough & Shukla, 1993). The capsid protein (CP) subunit of MDMV has a molecular weight of 28.5 × 103 (Hill *et al.*, 1973). The process of encapsidation and cell-to-cell transport is primarily performed by C-terminal regions of the coat protein and the flexible N-terminus is essential in long-distance and systemic transport while, it also contains the DAG motif essential for aphid transmission competence (Petrik *et al.*, 2010).

Transmission of virus

A short acquisition access period (AAP) of 10–30 s (Bancroft *et al.*, 1966) is found in MDMV. However, studies have revealed that a longer retention time can be found by increasing the acquisition time (Chauhan, 1985). The retention of the virus in the stylets of the vector is closely correlated to the transmission of the virus (Wang & Pirone, 1996). The virus particles can be retained directly or indirectly in the appendages of aphids before being inoculated into plants. The two viral encoded factors mediating the attachment of viruses to the appendages of aphids are the capsid protein (CP)-the component of the virion, and the helper component proteinase (HC-Pro) (helper component is a non-structural protein found only in diseased plants) (Salomon & Bernardi, 1995). The interactions between the stylet of the vector and the virus coat protein formed by the HC-Pro protein perform its function as a "molecular bridge" (Figure 1) (Pirone & Blanc, 2003). A triplet 3-amino acid sequence, DAG (Asp–Ala–Gly), near the N-terminal region of the coat protein, links to the transmission of potyviruses (Nault, 1997). Due to the unavailability of the N-terminus to interact with the aphid's stylet thus, the presence of HC-Pro is needed to cause a structural change to unfold the N-terminus of the coat protein. For aphid transmission, the DAG triplet in the N-terminal region of the coat protein is crucial (Atreya *et al.*, 1990) so, the substitution of any of the 3 amino acid residues can minimize aphid transmission radically. It is believed that the inoculation and retention of non-persistent viruses are localized at the distal edge of the stylet bundles (Wang *et al.*, 1996); however, the assumptions are not verified till now. Several factors influence the transmission of the virus. First, it is influenced by the fasting condition of the aphid. The fasted aphids transmit the virus much more effectively than non-fasted aphids (Stoner *et al.*, 1964).

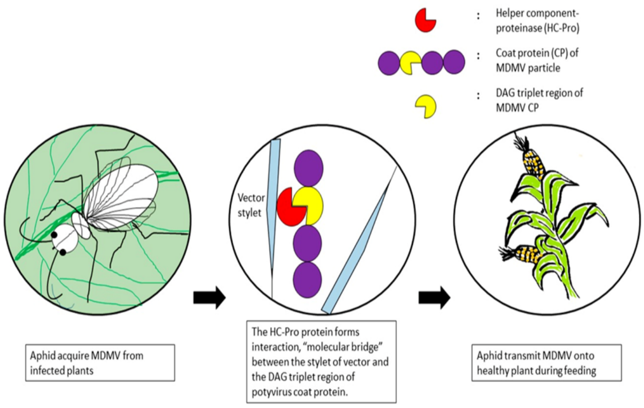

Figure 1. *Interaction between MDMV and vector appendage (Source: Kannan et al., 2018).*

Fasting enhances the virus retention in aphids as it allows the plant components to be swallowed or egested by clearing the alimentary canal (Atson & Oberts, 1939). Secondly, the transmission is influenced by the age of the plant leaf. The older the leaf, the lower the concentration of the MDMV, resulting in decreased aphid transmission (Stoner *et al*., 1964). Further, the transmission is related to virus concentration in maize, so any factors such as temperature, nutrition, or infection period may affect the virus transmission directly or indirectly (Stoner *et al*., 1964).

Symptoms of viral infection

Plants infected by MDMV exhibit mosaic patterns. This pattern initially appears on the youngest leaves near the lower regions, uneven and diffused (Cao *et al*., 2011). Mosaics appear as striped as they occur between leaf veins (Tsai & Falk, 2022); they develops as yellowish streaks running throughout the edge of the leaf, and later in subsequent growth seen as common chlorosis (Cao *et al*., 2011). When the chlorotic regions combine, forming continuous streaks along the veins, it forms a chlorotic band or an "A" shape. Chlorotic appearance on the upper leaves is the only visible symptom in older plants which may develop as red streaks at late infections (Teyssandier *et al*., 1983). Irregular necrotic lesions and mottling spots are the other symptoms (Jones *et al*., 2011*)*. The appearance of dark and light green mottles on the leaves are seen as early symptoms while, flecks, mosaics, and rings on the leaves are observed as the intensity of dark and light green mottles increases (Tsai & Falk, 2022). The immature growth stage infection causes a delay in maturity and the loss of a large number of kernels at the basal end of the ear, known as butt blanking (Gregory & Ayers, 1982). Likewise, MDMV infection causes a decrease in plant weight, decrease in ear weight, stunting, and delay in silking, and may also cause poor grain fill (Jones *et al*., 2011).

Management of maize leaf aphids by IPM

The principle of IPM is based on four major management practices: physical control, cultural control, biological control, and chemical control (Flint, 2012). The IPM practice integrates the management strategies such that the insect population remains below the economic threshold and in a manner that is economically sound and environmentally friendly (Ehler, 2006). The gradual adoption of IPM for the management of aphids results in high economic returns in the long term (Song & Swinton, 2009). One of the important aspects of IPM is monitoring and record-keeping. This allows farmers to implement a conducive management approach as per the need and status of the pest and its damage (Ehler, 2006).

Monitoring: To monitor for aphid infestation, plants should be regularly checked, at least twice a week at a rapidly growing stage, to catch infestations early. The greatest damage is caused when the temperatures are warm; when the density of aphids exceeds it causes leaves to curl and distort, providing shelter for aphids to hide, resulting in the ineffectiveness of natural enemies and insecticide application (Flint, 2016).

Physical control: The application of mechanical or manual methods to kill the pests or cause disturbance in their behavior is known as physical control of management. Some of the methods of physical management that can be applied to control aphids are the use of traps, fencing, or screening the greenhouse (Flint, 2012), spraying the plant with a jet of water, or removing the infected plant parts (Buss, 2006).

Biological control: Biological control of insect pests in IPM includes the introduction and conservation of natural enemies to control the pests population below the economic threshold level (Kenis *et al*., 2017). This natural enemy includes parasitoids, predators, and occasionally pathogens and vertebrates (Kenis *et al*., 2017). Various parasitic wasps lay their eggs inside aphids, turning the skin of parasitized aphids crusty and golden brown, known as mummies (Sarwar, 2017). Many predators, including lacewing larvae, lady beetle larvae and adult, syrphid fly larvae, and soldier beetles, feed on aphids (Flint, 2016).

Cultural control: Cultural control includes the farming practices that play roles in maintaining the pest population below the threshold level (Tang *et al*., 2005). One of the major sources of maize leaf aphids is the weeds, Johnson grass (Thongmeearkom *et al*., 1975), barley, and sorghum (Drost *et al*., 2020) near the maize field; weed management is one of the cultural practices to control the aphid population. Likewise, high nitrogen fertilizer in the crop favors the intensification aphid population. Thus, it is advised to supplement fertilizers in split doses (Morales *et al*., 2001).

Chemical control: In IPM chemical insecticides and pesticides are used only when needed and in combination with other approaches; the use of chemical pesticides is done in a way that minimizes the deleterious effects of chemicals on human health, non-target organisms, and the environment (Peshin & Zhang, 2014). Insecticidal soaps and oils (petroleum-based horticultural oils or plant-derived oils such as neem oil or canola oil) are the best choices for the management of maize leaf aphids because these insecticides leave no toxic residues and are less harmful to natural enemies (Flint, 2016).

Conclusion

In conclusion, the intricate interplay between maize, its insect vectors like the maize leaf aphid, and the Maize Dwarf Mosaic Virus (MDMV) underscores the necessity for a multifaceted approach to disease management. Maize stands as a critical global crop, essential for food security and various industrial applications, making it imperative to safeguard its health against the threat of viral diseases transmitted by aphids. Integrated Pest Management (IPM) emerges as a pivotal strategy, integrating diverse management practices to maintain aphid populations below economic thresholds while minimizing environmental impacts. Regular monitoring and meticulous recordkeeping are emphasized as fundamental components of IPM, enabling farmers to respond promptly to changing pest dynamics and crop conditions. By closely monitoring aphid infestations, interventions can be implemented at the earliest signs of trouble, preventing population explosions, and minimizing crop damage. Additionally, IPM advocates for the adoption of cultural practices that create unfavorable conditions for aphids, such as weed management and judicious fertilizer application. These practices not only help control aphid populations but also promote overall crop health and resilience. Biological control methods are highlighted as effective and environmentally sustainable means of managing aphid populations. By introducing natural enemies like parasitic wasps and predators, farmers can leverage nature's own mechanisms to keep pest populations in check. This approach not only reduces reliance on chemical pesticides but also helps preserve beneficial insect populations and ecosystem balance. When chemical control is deemed necessary, it should be approached with caution and used in conjunction with other management strategies. Preference should be given to safer options like insecticidal soaps and oils, which leave minimal residues and pose fewer risks to non-target organisms and the environment. Continued research into virus transmission mechanisms and symptom development is crucial for developing innovative management strategies that ensure the long-term sustainability of maize production and global food security. By gaining a deeper understanding of plant-insect-phytopathogen interactions, scientists and farmers can devise targeted approaches to disease management that minimize economic losses and environmental impacts while ensuring the continued productivity of this vital crop. Despite significant research efforts aimed at unraveling the plant-vectors-pathogen interaction, there is still limited scientific knowledge of the molecular mechanisms mediating specific vector-borne diseases. To fill the knowledge gap and be able to engender novel strategies to control vector-borne diseases, there is a need to increase scientific research on the molecular level that involves specific vectors, their roles in virus transmission, and disease development in plants. Likewise, studying molecular interactions provides knowledge on the genes and molecules that can be targeted as part of genetic pest control strategies and used to successfully disrupt pathogen transmission by insect vectors to host plants. The developing countries are far behind in sophisticated tools and knowledge to carry out the study of vector-borne diseases on the molecular level. As a matter of fact, in developing countries, the growth rate of food production is far below the growth rates of demand, and food imports are growing faster than their agricultural exports (FAO, 2002). So, there is a need to intensify the scientific study and research on different geographic regions on the molecular basis of plant, vector, and pathogen interaction to unravel novel strategies to combat vector-borne diseases and sustain the global food system.

Conflicts of interest: The authors declare no conflict of interest.

Ethical approval: Not applicable.

Data availability: The data that support the findings of this study are available on request from the corresponding author.

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