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Review

Aphid–Plant–Phytovirus Pathosystems: Influencing Factors from Vector Behaviour to Virus Spread

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Abstract: Aphids are responsible for the spread of more than half of the known phytovirus species. Virus transmission within the plant–aphid–phytovirus pathosystem depends on vector mobility which allows the aphid to reach its host plant and on vector efficiency in terms of ability to transmit phytoviruses. However, several other factors can influence the phytoviruses transmission process and have significant epidemiological consequences. In this review, we aimed to analyse the aphid behaviours and influencing factors affecting phytovirus spread. We discussed the impact of vector host-seeking and dispersal behaviours mostly involved in aphid-born phytovirus spread but also the effect of feeding behaviours and life history traits involved in plant–aphid–phytovirus relationships on vector performances. We also noted that these behaviours are influenced by factors inherent to the interactions between pathosystem components (mode of transmission of phytoviruses, vector efficiency, plant resistance, …) and several biological, biochemical, chemical or physical factors related to the environment of these pathosystem components, most of them being manipulated as means to control vector-borne diseases in the crop fields.

Keywords: host selection; plant–aphid–virus pathosystem; vector activity; vector-born virus; vectorial transmission efficiency

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1. Introduction

Phytoviruses are an important group of phytopathogenic agents. They are responsible for major crop yield losses estimated at around USD 60 billion annually worldwide [1]. They are obligate parasites, mainly composed of genetic material (nucleic acid: RNA or DNA) within a protein shell (capsid). Due to this minimalist constitution, phytoviruses are unable to reach new hosts. However, they must switch from one plant to another before the previous one dies in order to survive [2,3]. So, phytoviruses have developed various dispersal strategies, most importantly relying on vectors [2]. Several groups of fungi, nematodes, mites and insects play this role. Herbivorous insects are known to be vectors of most phytoviruses due to their mobility and behaviour allowing them to circumvent plant immobility in order to spread [2,4]. Various insect orders are recognised as phytoviruses vectors, such as Coleoptera, Orthoptera, Lepidoptera, Dermaptera, Diptera, Thysanoptera [5], but especially Hemiptera [6]. Aphids (Hemiptera: Aphididdidae) are by far the most important phytoviruses vector group. They are involved in spreading more than half of the known phytovirus species (275 species within 19 genera) [5]. Consequently, this review will focus especially on aphids.

The classification of phytoviruses is based on their mode of transmission. It takes into account three events: (1) acquisition during the insect meal on an infected plant; (2) retention or circulation within the insect vector organism; and (3) inoculation during a new insect meal on a healthy plant [1,7]. These three events occur in different ways, resulting in several classifications of phytoviruses discussed in [5]. In this review, we have chosen

the classification taking into account the site and retention time of phytoviruses in insect vector organisms. Then, we distinguish phytoviruses transmitted by non-circulative and circulative modes. (1) Non-circulatively transmitted phytoviruses are limited to the tips of the stylets (non-persistent or stylet-borne viruses) and foregut (semipersistent or foregut-borne viruses) of the vector [8]. These phytoviruses are acquired and transmitted during short probing punctures by the insect vector in plant epidermal and mesophyll cells. After acquisition, the vector becomes directly infectious within minutes to a few hours or during many hours for non-persistent and semipersistent phytoviruses, respectively [5]. (2) Circulatively transmitted phytoviruses require a long-lasting sap ingestions phase, followed by an incubation or latent period. During this period, the phytovirus is ingested and circulates in its vector's organism until it reaches its salivary gland (persistent or salivary gland-borne). Then, the vector becomes able to transmit the phytovirus for at least several days, or even its whole life-cycle [2,5].

The phytovirus transmission process by insect vector rely on two mains steps: firstly, the vector activity, comprising host-seeking, feeding and shifting or dispersal behaviours; secondly, the vector efficiency depending on their intrinsic ability to transmit phytoviruses [9]. Furthermore, several factors related to the phytovirus and/or the host plant, but also the insect–plant–phytovirus interactions can influence the phytoviruses transmission process and have significant epidemiological consequences [6]. Phytoviruses have been demonstrated to use different mechanisms to improve their spread, including manipulating their vector's activity and transmission efficiency directly or through their shared host plants [9]. Life history traits can provide indications of how the vector benefits from the relationship between the components in the interaction [3]. There are also external factors from the pathosystem components that can influence the epidemiology of viral diseases. These include biotic and abiotic factors, used for experimental purpose or resulting from crop protection strategies.

Given the potential impact of the above on the epidemiology of insect-vector-borne phytovirus diseases, a better understanding of insect vector activity, transmission efficiency and factors responsible for their alterations may allow the development of more effective crop protection strategies. In this review, we analyse the current knowledge in the vector activity, the vector transmission efficiency as well as the vector's life history traits on plant–aphid–phytovirus pathosystems. We highlighted factors that have been presented as causing changes in these aphid behaviours and life history traits that could enhance phytovirus spread.

2. Vector Activity in Aphids

Vector activity is related to a set of behaviours on which the phytovirus relies on reaching new hosts. It includes host-seeking behaviour (HSB), probing and feeding behaviour (FB) and dispersal (or shifting) behaviour (DB). Except for FB, vector activity is closely linked to the displacement of the insect towards its host plant. Then, knowing how they move themselves will provide a better understanding of how they reach their host plant to spread phytoviruses.

Aphid life cycles are known to be diversified with several morphological forms associated to different host plants according to the season and environmental conditions (see the review in [10] and Figure 1). Depending on their mobility, adults are either winged or wingless. Winged morphs, especially spring and summer migrants, are known to be important in conquering new hosts, establishing new colonies and, at the same time, responsible for spreading phytoviruses over long distances. Spring migrants transmit phytoviruses acquired from alternate hosts in early spring to crop plants while summer migrants transmit phytoviruses within the field from one plot to another, more or less distant, during plant-to-plant movements over several generations [11]. As for wingless, they spread the infection by walking from one plant to another in the vicinity of the initially colonised plant [12]. Finally, fall migrants are involved in the transmission of new phytoviruses which were acquired in the field from distant sources to the alternate hosts

(reservoir plants) [11]. Therefore, the emergence of winged forms would be favourable to the further phytoviruses spread.

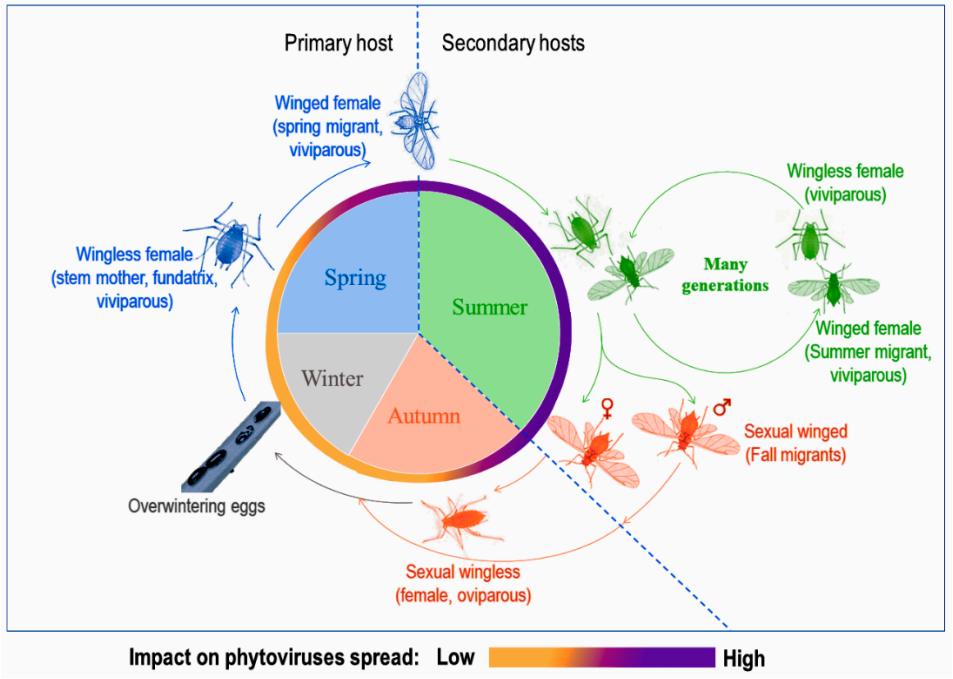

Figure 1. A representation of a dieocic aphid life cycle with at least two plant hosts and its impact on phytoviruses spread, adapted from [11,13].

2.1. Host-Seeking Behaviour (HSB)

Depending on the vector's location and the ways in which it communicates with its host plant, the HSB can be categorised into the following three phases: (1) pre-contact, (2) post-contact, and (3) acceptance (Figure 2).

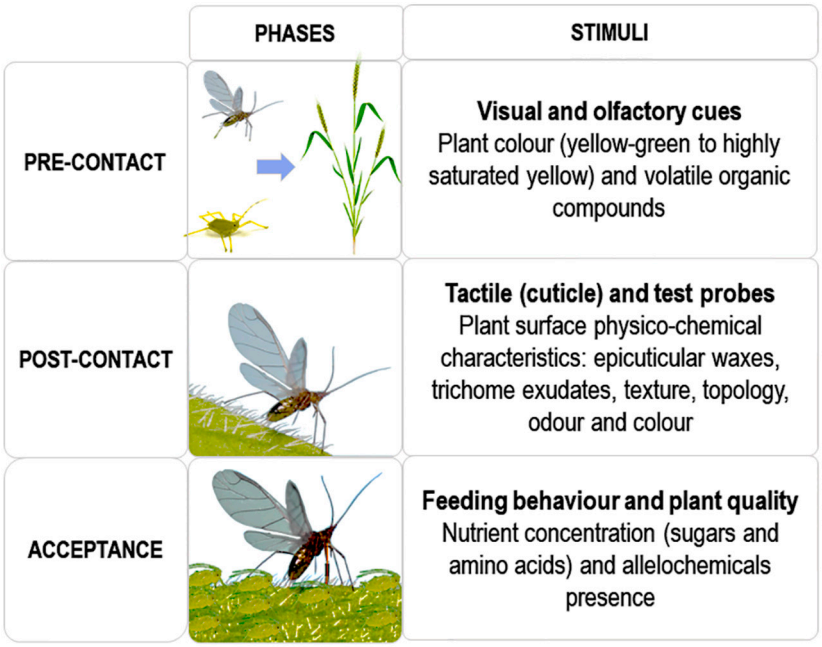

Figure 2. Summary of 3 phases of host-seeking behaviour and the stimuli involved, adapted from [14].

2.1.1. Pre-Contact

During the pre-contact stage, aphids are guided by the perception of visual and olfactory stimuli. Thanks to their compound eyes equipped with ocular photoreceptors, aphids react to reflections of light beams from different sources and orient themselves on what they identify as their host plants. It has been shown that winged aphids have well-developed compound eyes compared to wingless, but the difference in the perception of visual stimuli remains to be defined [15]. However, intermorph variation is demonstrated in relation to the olfactory cue. Indeed, the olfactory cue is perceived by sensory structures called rhinaria located on the tips of aphid antennae [16]. Wingless aphids are equipped with primary rhinaria, i.e., detecting only host plant odours, whereas the winged individuals have secondary rhinaria, which are more evolved, perceiving host and non-host volatile chemicals [16]. This would be due to the fact that winged aphids fly over a broader range of plant species that they need to be able to distinguish from their host plant on which they should land [17].

Bioassays assessing the pre-contact HSB of aphids are adapted according to the kind of insect morphotype. For example, pre-alighting behaviour is assessed in winged aphids [5]. This consists of tracking insect flight behaviour in response to visual and/or olfactory stimuli using a flight tunnel [18]. It has been established that aphids are able to target and land on yellow or yellow–green surfaces, but preferentially on highly saturated yellow surfaces under low wind conditions in the absence of plant odours [3,5,19]. Yet, yellowing is among the typical plant symptoms associated with phytovirus infection. This is the case for cereal/barley yellow dwarf virus (C/BYDV) [20–22], phytoviruses causing mosaic diseases, such as cucumber mosaic virus (CMV) [23], pea enation mosaic virus (PEMV) [24]. Additionally, Hodge and colleagues [24] reported that *Acyrthosiphon pisum* (Harris, 1776) was highly attracted to older *Pisum sativum* L. with well-developed symptoms of PEMV, probably in response to visual cues from the yellowed and mottled infected leaves. Leaf yellowing has long been considered as a phytovirus strategy to attract new vectors, especially aphids, to ensure its spread [20,25]. For testing only the visual cue in pre-contact HSB, plants are sometimes replaced by light beams [19,26,27].

Regarding odour cues, it has also been shown that the plant volatile organic compounds (VOCs) are qualitatively and/or quantitatively modified following phytovirus infection [20,28]. Indeed, infected plants generally become more attractive, especially compared to insects not carrying phytovirus [29]. Rajabaskar and colleagues [30] demonstrated that potato leafroll virus (PLRV) infection-induced changes in total headspace VOCs from potato plants that altered the pre-contact HSB of *M. persicae*.

To assess the impact of odour cue on the pre-contact HSB of aphids, various methods were used: either a plant in darkness [31], or natural or synthetic VOCs, single or mimicking the plant's odour profile [20,31,32]. Olfactometers are also well adapted for assessing the impact of odour cues, without interference from visual cues even if some devices based on the position of the insect relative to the odour source did not provide full details of the insect's behaviour. Indeed, VOCs can have attractive or repulsive effects, but can also induce arrestment in aphids. Ngumbi and colleagues [33] reported that the individual component β-pinene from potato plants (*Solanum tuberosum* L.) infected with PLRV induced arrestment behaviour rather than attraction to *M. persicae*. In contrast, *Rhopalosiphum padi* L. was attracted by BYDV-infected wheat, according to the results presented by Medina-Ortega and colleagues [34].

The effects of VOCs on the pre-contact HSB of aphids are observed in both winged and wingless aphids. Particularly, arrestment behaviour is found when insects move by walking [35]. Circular arenas are most commonly used to observe this behaviour, using intact leaves attached to or cut from the mother plant, but also using leaf discs [35]. These arenas must prohibit insect access to the plant in order to analyse only the odour cue response [35]. However, trials that allow insects access to the plant are closer to natural conditions. They permit to analysis of not only visual and odour but also the tactile cues.

2.1.2. Post-Contact

Interactions between host plant and aphid based on visual and olfactory stimuli are not specific enough because they take place from a distance. The tactile stimulus is therefore used for more specificity. After landing, or when reaching the plant by walking, physico-chemical characteristics on plant surface influence insect behaviour [36]. These include epicuticular waxes, trichome exudates, texture, topology, odour and colour on the plant surface [36]. On one hand, basic non-specific ways allow to some plants to resist against aphid infestation. On the other hand, they are used by aphids to recognise their host plant before making test punctures to find the feeding site [37].

Test punctures play an important role in the recognition process of host plant by insects [38]. The aphid briefly inserts and removes its stylet several times into the plant epidermal cells. In the background, the insect exchanges with the host plant, causing a battery of chemical and biochemical reactions, resulting in two possible outcomes: (1) either the insect finds the feeding site and initiates sustained phloem ingestion, in which case there is host plant acceptance (see acceptance); or (2) the insect may encounter resistance that inhibits its ability to feed successfully on the plant on which it has landed.

As a consequence of test punctures, the plant reacts by activating its defence systems that may make it unsuitable host for aphids. These defence systems target the insect and/or probably the pathogen that the insect is carrying [39]. Several mechanisms could mediate this resistance. The most basic are those mediated by the well-known phytohormones signalling pathways, jasmonic acid (JA), salicylic acid (SA) and ethylene (ET). They include cell membrane modification and increases in insect-damaging compounds, including secondary metabolites, protein inhibitors and repellent VOCs [37]. Other mechanisms such as the deposition of calloses, lignin, and other phenolic compounds are deployed by plants in response to aphid feeding (Sun et al., 2018). However, there is evidence (well documented in [37]) that aphids and other phloem-feeding insects can manipulate these plant defence pathways, sometimes with the assistance of pathogens they transmit. Studies compiled in [40] have shown that aphids reprogram the plant's defence strategy to improve its fitness. They inhibit efficient plant defence mediated by JA pathway, allowing the SA pathway, without effect on aphid feeding but preventing pathogen infections. Moreover, there are viral proteins that may interfere with the host plant defence system to improve the plant suitability encouraging aphid sustainable phloem feeding. This is the case for PLRV proteins P0, P1 and P7, which were identified in infected *Nicotiana benthamiana* [41]. In presence of aphids, both P0 and P1 inhibited SA and JA induction compared to control plants, whereas ET emission from aphid free plants were inhibited by P7 on PLRV infected plants compared to control [41]. However, this may not happen every time in all pathosystems in the same way depending on plant cultivars and aphid species [40]. In some cases, more specific resistance mechanisms can also be used by plants. This is illustrated with glucosinolates synthesised by *Brassica* plants to cope with pathogen and herbivore attacks [37]. All these kinds of resistance can reduce plant palatability, feeding deterrence and toxicity [37], and consequently reduce the insect fitness and encourage them to disperse to other plants (see Section 2.3). This is known as host plant rejection [38].

Post-contact in aphids HSB is a very important step in the plant–insect–phytovirus relationship and has an important impact on the epidemiology of vector-borne viruses. Indeed, regardless of the outcome of the aphid's test punctures on plant, this corresponds to most non-circulative phytoviruses acquisition and transmission [8,42]. Moreover, this is an efficient strategy by viruses to improve the dispersal behaviour of their vectors in order to spread.

2.1.3. Host Acceptance or Selection

Host plant acceptance is an ultimate and crucial result of aphid HSB. It can be observed within two main parameters: firstly, feeding behaviour (see next section). Host acceptance or selection occurs when the insect does not encounter or successfully circumvents plant resistance and extends its phloem-feeding period [43]. It can be assessed more accurately on an individual scale by taking into account parameters that may determine how easy it is for the insect vector to feed on a given plant. Then, the quality of consumed food is of paramount importance at this stage. This is in terms of nutrient concentration, especially sugars and amino acids, but also regarding to the absence of deterrent allelochemicals affecting ingestion and aphid performance [44].

Secondly, the aphid performance includes all traits assessing the insect's fitness on plant including reproduction or larviposition and more life history traits. Host acceptance implies an active decision to settle and establish a colony on a plant [45]. It is characterised by a high reproductive rate, optimal growth rate and development time, high survival rate, prolonged longevity resulting in high population growth. All these parameters are discussed in Section 4 on aphid life history traits and the factors involved in their modulation in plant–aphid–phytovirus pathosystems.

2.2. Probing and Feeding Behaviour (FB)

From the search for a feeding site to sustained phloem-feeding, aphids penetrate the plant with their stylets while salivating. They reach different plant tissues in several stages, in particular xylem and phloem, where they feed by sucking sap. These different stages specifying the activities of the stylets and the time spent in different plant tissues define the aphid FB. The latter is studied using an electropenetrography (EPG) system (Figure 3). Electrical waves generated by stylet activities in plant tissues are amplified and recorded on a computer. Combined with histological sections, patterns of EPG waveforms have been associated with different stylet positions in plant tissue and feeding activities [46]. Seven waveforms for aphids were defined by Tjallingii and Prado [47]: (1) probing (probe) and non-probing (np) waveforms; (2) intercellular stylet pathway and salivation (C); (3) potential drop (pd) caused by intracellular stylet punctures during C phase; (4) salivation into phloem (E1); (5) passive phloem sap uptake (E2); (6) active intake of xylem sap (G); and (7) stylet penetration difficulties (F) [3,6,48]. These parameters refer to the analysis of EPG variables corresponding to the duration and number of occurrence of events generating different waveforms (non-sequential parameters) as well as sequential parameters related to specific sequences of these waveforms. More than one hundred and twenty variables can be analysed in aphid FB study, which can be found in [49].

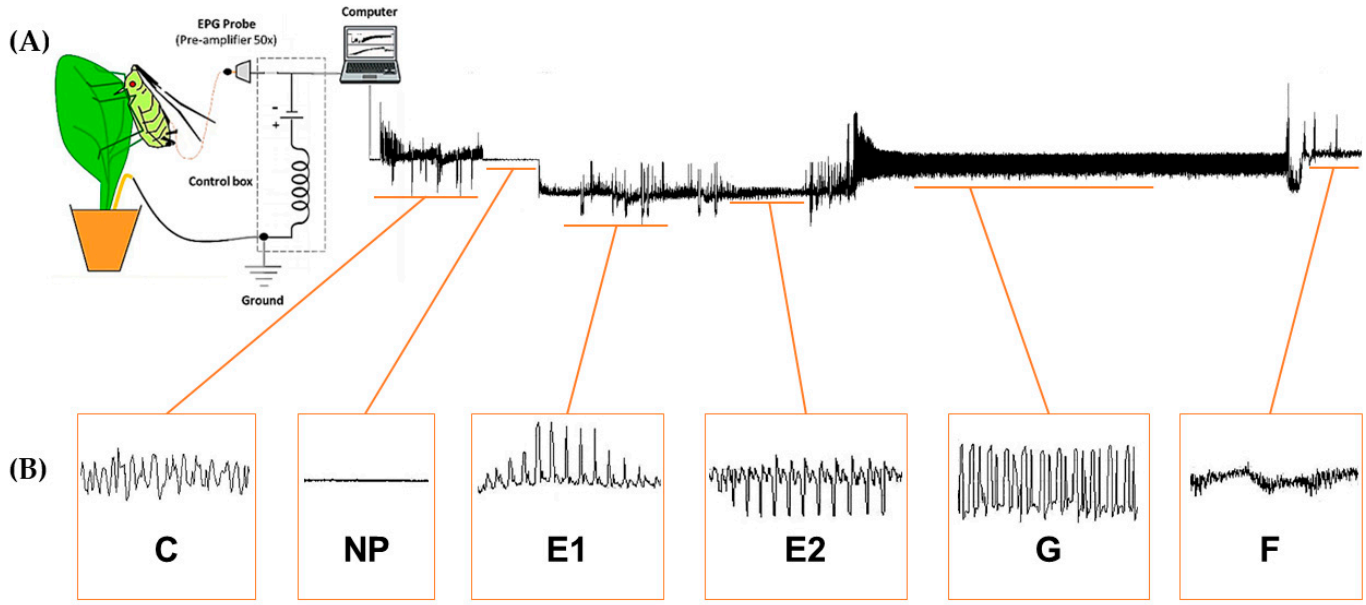

Figure 3. Analysis of aphid feeding behaviour by electropenetrography. (**A**) EPG system set-up with waveform pattern; (**B**) typical waveforms corresponding to different feeding phases; C: intercellular stylet pathway and salivation; pd: potential drop; E1: salivation into phloem; E2: passive phloem sap uptake; G: active intake of xylem sap; F: stylet penetration difficulties.

Based on this knowledge, scientists have been able to describe the characteristics of sustainable sap ingestion that predict host plant acceptance. Indeed, the number of probe and np phases before first phloem phase are considered as important events in host plant recognition and acceptance [38]. Several probes are needed between 3 and 4 h after plant access prior to long sustained phloem sap ingestion, which should include more than 10 min of the E2 phase [50]. Moreover, knowing the different types of phytoviruses according to their location in plant tissues as well as their modes of acquisition and transmission, EPG waveforms analysis allowed to determine the phases of aphid FB corresponding to acquisition and/or transmission of circulative and non-circulative phytoviruses during the brief (3–6 s) intracellular punctures corresponding to the pd waveform of the EPG system [51–53]. Boquel and colleagues [9] used the observation of the first pd waveform to determine the acquisition access period (AAP) of potato virus *Y* (PVY) from seven aphid species. Furthermore, the E2 and E1 phases correspond to the acquisition and inoculation of phytoviruses transmitted by the circulative mode, respectively [38,47].

Several studies based on the analysis of EPG parameters have noted the alteration of aphid FB associated with the infectious state of the insect and/or the host plant that may influence the phytovirus spread. Circulative phytoviruses influence directly or indirectly (via the host plant) the E1 and E2 phases to improve their propagation. For viruliferous insects, the E1 phase is prolonged on healthy plants, likely to improve the transmission of phytoviruses, whereas, for non-viruliferous insects feeding on phytovirus-infected plants, the E2 phase tends to be prolonged. This was reported by Carmo-Sousa et al. [6], based on the FB of *Aphis gossypii* Glover on *Cucumis sativus* L. and *Gossypium hirsutum* L. infected with cucurbit aphid-borne yellows virus (CABYV, circulative phytovirus). Similarly, Angelella and colleagues [54] noticed that pd phases recorded when *Aphis craccivora* Koch fed on Pumpkin (*Cucurbita pepo* L.) infected with watermelon mosaic virus (WMV: non-circulative phytovirus) were significantly higher than on the healthy plant. Similar

observations were reported by Carmo-Sousa and colleagues [6] when *A. gossypii* was placed on *C. sativus* L. infected or not with CMV (non-circulative phytovirus). However, in the latter study, this significant difference was observed when EPG variables were analysed at short time intervals (0–15 min). In contrast, no significant difference was recorded in the 15–30 min interval frame illustrating manipulation by non-circulative phytoviruses of the FB of their vector in order to induce them to migrate to new plants for propagation.

Furthermore, the FB of different insect species, or even different biotypes of the same vector species, can be differentially impacted by phytovirus infection. For example, PVY induced a significant increase in the NP phase and decrease in the C and E2 phases in *M. persicae* when feeding on infected plant compared to the healthy plant, while in *M. euphorbiae*, there was rather a decrease in the NP phase and increase in the E2 phase in PVY-infected plants and no significant difference for the C phase [55]. Moreover, four isolines of *A. craccivora* from *Robinia pseudoacacia* L. and *Medicago sativa* L. exhibited different C phase frequency on *C. pepo* infected with WMV [54]. This would be related to the presence and absence of endosymbiont microorganisms as well as other biotic and abiotic factors, see Section 5.

2.3. Shifting or Dispersal Behaviour (DB)

Dispersal behaviour is defined as the switching habit of an insect from one plant to another. In the epidemiological context of aphid-borne phytovirus diseases, vector DB plays an important role in the spread of phytoviruses. It represents the vector activity which, together with the transmission efficiency (see Section 3), is dependent on the duration and extent of the association between the phytoviruses and their vectors (vector efficiency) and the environmental conditions and determines the potential impact of the spread of such phytoviruses [46,56].

The relationship between circulative phytoviruses and their vectors is described as mutualistic and may have co-evolved resulting in an improvement of the vector's fitness, the latter ensuring virus propagation [29,57]. The improvement of the vector's fitness is achieved by increasing the plant quality and palatability for insects [6,25]. Then, the plant gains attractiveness to the vector in order to acquire the phytovirus and promotes vector population growth. The latter could result in overcrowding of insects on the same plant, leading to the emergence of winged morphs (summer migrants) in aphids, responsible for the long-distance spread of phytoviruses [58].

An increasing literature showed that circulative phytoviruses directly manipulate the preference of their vectors in order to orient them towards healthy plants. Rajabaskar and colleagues [28] found that virus-free *M. persicae* were attracted to PLRV-infected potato plants but, after acquisition of phytovirus, this attractiveness was reversed, with the newly viruliferous aphids moving to healthy plants. Similar results were obtained by Ingwell and colleagues [59] with *R. padi*–wheat–BYDV pathosystem. However, this latest study reached a new level by eliminating any potential interference from factors related to infected plants, by testing aphids for virion acquisition when feeding on an artificial medium [60]. This provides further evidence that phytovirus is responsible for this DB. During their acquisition, circulative phytoviruses travel through their vectors' organism encountering and traversing a diversity of membrane barriers in different tissue systems from the midgut to the salivary glands. Then, they may target the host's neural, endocrine, neuromodulatory, and immunomodulatory systems during infections influencing directly its behaviour [60].

Conversely to what has been described above, non-circulative phytoviruses do not have a strong link with their vectors. Indeed, when they are acquired, they bind to the vector stylet or midgut for a relatively short period. Non-circulative phytoviruses rather act with indirect influence on their vectors by passing through the shared host plant. As with circulative, non-circulative phytoviruses also enhance plant attractiveness, notably through visual and olfactory features. Black raspberry necrosis virus (BRNV) and

raspberry leaf mottle virus (RLMV) manipulated the behaviour of the raspberry aphid, *Amphorophora idaei* Börner by enhancing the concentration of the attractiveness compounds (Z)-3-hexenyl acetate on infected red raspberry (*Rubus idaeus* L.). Well-developed symptoms of PEMV induced a strong preference to *A. pisum* probably in response to visual cues [61]. However, non-circulative phytoviruses reduce the plant suitability for its vectors in order to encourage them to visit other plants for its spread. They reduce or at least do not improve plant palatability in order to discourage its vectors from long-term feeding because of the risk of losing their infectivity [56]. For example, infection of *Arabidopsis thaliana* (L.) Heynh with CMV had induced the biosynthesis of 4-methoxy-indol-3-yl-methylglucosinolate (4MI3M), inhibiting phloem ingestion for *M. persicae* [62]. In addition, several studies had shown that aphid settling preference and life history traits were less favourable on plants infected with non-circulative phytovirus [3,31,63,64].

Bioassays assessing the DB of aphids often aim to determine the potential impact of the spread of phytoviruses. This impact is related to the mode of transmission of phytoviruses: high aphid vector activity is favourable for the spread of non-circulative phytoviruses, while it is unfavourable for the spread of circulative phytoviruses [56]. For example, Dáder and colleagues [8] found that an induced dispersal of *A. gossypii* carrying CMV or CABYV transmitted in non-circulative and circulative manner, respectively, led to an increase in CMV spread in the short term, while the spread of CABYV was significantly limited. A similar finding was reported by Lin and colleagues [12] with *M. persicae* and *M. euphorbiae*, both transmitting PVY and PLRV in non-circulative and circulative manners, respectively. Here, there was a trend of decreased PLRV spread, without being significantly different from the control where there was no stimulation of insect dispersal. Furthermore, Belliure and colleagues demonstrated that non-circulative phytovirus propagation was proportional to the level of disturbance in aphid colonies [65]. Finally, phytoviruses control the DB of their vectors to allow them to optimise their propagation by adapting the mechanism according to both transmission ways.

3. Vectorial Transmission Efficiency

Vectorial transmission efficiency (VTE) is the probability of obtaining plants infected by a given phytovirus using a given vector under well-defined environmental conditions [66]. It relies on two main components: (1) vector efficiency, which is defined as the intrinsic capacity of a vector to transmit one or more phytoviruses, and (2) interference of factors related to experimental methods and biological materials when assessing VTE.

3.1. Vector Efficiency

Vector efficiency (VE) refers to the interaction between a phytovirus and its vector. This interaction is characterised by a given level of specificity of transmissibility such that a phytovirus recognises its vector, or especially, the virion or a viral protein motif recognises the site of retention upon acquisition by its vector. This specificity level in different pathosystems can be exclusive, i.e., one vector transmits only one phytovirus species and this virus has a single vector (the case of grapevine fan leaf virus (GFLV), transmitted by the nematode *Xiphinema index*), or very broadly: one genus or species of phytovirus has several vectors or one vector is involved in several pathosystems [67]. For example, on the one hand, the whitefly *Bemisia tabaci* transmits several phytoviruses of different genera and families and, on the other hand, the Closteroviruses are transmitted by several groups of insects including mealybugs, whiteflies and aphids. In aphids, Potyviruses are transmitted by more than thirty species [67]. *Myzus persicae* is a vector of more than hundred phytoviruses belonging to different genera and families [13]. It should be noted that, when a phytovirus is transmitted by several vectors, one is recognised as the most efficient vector, making it a reference vector for transmitting this phytovirus. This is the case of *M. persicae* which serves as a reference vector for PVY, on the basis of which the relative efficiency factors (REFs) of the remaining vectors of this phytovirus are evaluated [9,59].

The specificity in the vector–phytovirus relationship described above is regulated by determinants which at the same time regulates the transmissibility of each phytovirus by its vector. These determinants depend on the mode of transmission (circulative or non-circulative), the site of retention (stylet-born or foregut-born or salivary gland-born phytoviruses) and the strategy adopted by the phytovirus [68]. For stylet-born phytoviruses (non-circulative, non-persistent), there is either the strategy of direct attachment and retention of the virion on the putative receptors on the stylets of the vector; or the phytovirus uses helper components serving as intermediates between the virion and the vector's receptors on its stylets (Blanc et al., 2014). The latter strategy is used by Potyviruses and Caulimoviruses where the helper component is designated as HC-Pro and P2, respectively [69]. As for the foregut-born (non-circulative, semi-persistent) phytoviruses, this is called a capsid binding strategy using the minor capsid protein (CPm). This is the case for Criniviruses [70]. Finally, the salivary gland-born (circulative, persistent) phytoviruses bind to the receptors of their vectors mainly through their coat protein [68].

3.2. Interference Factors of Biological Materials and Experimental Methods

When performing bioassays evaluating VTE in a given pathosystem, the result interpretation must take into account the biological material used., i.e., the use of the reference vector or the one whose REF is closer to one compared to phytovirus under study will allow to attainment of higher infection rates compared to a less efficient vector [9]. For example, *M. euphorbiae*, often considered as the most efficient potato-colonising aphid vector of PVY, will provide infection rates close to those that would be obtained with *M. persicae*, the reference vector in this pathosystem [9,71]. However, the study aiming to establish REFs of seventeen aphid species with three different biotypes each for the transmission of three PVY strains (PVY^{NTN}, PVY^{NO}, and $PVY^{N\text{-}Wi}$) reveals that difference in VTE can also occur depending on the variability of biotypes within the same insect species and also of strains within the same phytovirus species [72]. For plants, VTE varies according to plant species status as main or alternative host of phytovirus and the associated vector [71], to resistant/susceptible character to phytovirus [73], but also according to plant phenology [71].

Several factors related to the protocol for monitoring the transmission process of a phytovirus by a vector on a plant can constitute sources of variation when performing VTE experiments under controlled conditions. In addition to above mentioned factors concerning the vector, its rearing conditions, growth stage and the number of individuals used to implement the test also influence the VTE results [9,72,74]. Moreover, it has been well established that individuals that previously underwent a pre-acquisition fasting period transmitted more efficiently the phytovirus compared to non-starved individuals [75–77]. Within the source plant, the phytoviruses concentration is not uniform [9,72]. It would be more concentrated on the plant younger top leaves, compared to older ones [74]. Finally, the AAP/IAP ratio can influence the VTE as reported by Sadeghi and colleagues [78] who found that a short AAP (6 h) followed by a long IAP (120 h) and a long AAP (48 h) followed by a short IAP (6 h) were the only factors to differ to the VTE of twenty *R. padi* clones transmitting BYDV-PAV isolate.

4. Life History Traits

Life history traits (LHT) are biological parameters that reveal the insect performance in a given environment. Several parameters are used to evaluate aphid performance, including reproduction rate, body growth, development time, survival rate, longevity, colony growth. In plant–aphid–phytovirus pathosystems, the aphid LHTs are indicative of the host plant–phytovirus relationship.

Circulative phytoviruses are known to encourage their vectors to colonise plants. The performances of aphids settled on plants infected with circulative phytoviruses is improved compared to those on healthy plants. This is the case of *Micromyzus kalimpongensis* Basu which had higher fecundity, faster growth rate during nymphal instars and longer

adult longevity on cardamom bushy dwarf virus (CBDV)-infected compared to noninfected plants enhancing colony growth [57]. Moreover, dos Santos and colleagues [20] had recorded 25% of *R. padi* population increase on BYDV-infected wheat than non-infected plants. Additionally, non-circulative phytoviruses discourage the vector settlement on infected plants, resulting in the deterioration of their LHT. For example, measurements of growing parameters carried out on *M. persicae* settling on a PVY-infected tobacco plant revealed a significant decrease in body and head width, body and cornicle length, and the gap between compound eyes [79]. Similarly, delayed body growth and prolonged development duration were reported for *A. gossypii* and *M. persicae*, respectively on CMV infected plants [3,62]. Reproduction rate and population growth rate of *A. idaei* were also negatively impacted on *R. idaeus* infected by RLMV or BRNV [80]. However, there are a few exceptional cases where vector settling performance on circulative and non-circulative phytovirus-infected plants has been reduced and improved compared to healthy plants, respectively. These were the cases of *A. gossypii*, vector of papaya ringspot virus (PRSV) on *C. pepo* [25] and *M. persicae*, vector of turnip yellows virus (TuYV) on *Camelina sp.* [44].

Aphid performance as vectors of phytoviruses on their respective shared host plants was generally related to plant quality, which can be categorised into the following two characteristics: (1) the nutrient content, especially sugar and amino acids; and (2) the presence/absence of toxins and feeding deterrents. The performance level of phytovirus vectors is often linked to the high nutrient content of host plant. For example, Gadhave and colleagues [25] demonstrated the positive effect of free essential (lysine, arginine and threonine) and non-essential (homocysteine and glycine) amino acids and soluble carbohydrates (cellobiose, raffinose and galactose) increase on *A. gossypii* performances. Nevertheless, the accumulation of certain amino acids can produce negative effects on some aphids. For example, weak performance of *A. idaei* presented in the previous paragraph would be due to the accumulation of glutamate on BRNV and RLMV infected plants. This would be a strategy used by these phytoviruses to induce vector dispersal [80]. Another strategy used by non-circulative phytoviruses is the biosynthesis of toxins and feeding deterrents. In Section 2.3, we discussed the case of 4MI3M, one aphid feeding-deterrent synthesised by CMV to discourage prolonged sap ingestion by vectors [62]. This resulted in a reduction in the *M. persicae* growth rate. When aphids were transferred from infected to healthy plants, there was no significant difference in growth rates between individuals from infected and control plants [62].

5. Factors Due to External Components from Plant–Insect–Phytovirus Interaction

Integrating additional components which are external to the plant–insect–phytovirus relationship may have an effect on different aspects of vector life that may influence the phytovirus spread. Biological, biochemical, chemical, and physical factors have been incorporated as a fourth level in the plant–insect–phytovirus relationship on an experimental basis or as a developing or already widely used plant protection tool in agriculture.

5.1. Biological Components

Various beneficial organisms in agriculture have been studied for their integration into crop protection strategies. These include macro-organisms such as parasitoids and predators, but also micro-organisms such as bacteria, fungi and viruses. In phytovirus pathosystems, the impact of the presence of some of these organisms has also been studied.

5.1.1. Macroorganisms

Several research axes are of interest on the integration of macroorganisms in phytovirus pathosystems. Firstly, the agroecosystem approach corresponds to studying aspects of multitrophic interactions where the performance of macroorganisms reproducing

and/or feeding on vectors, settling on phytovirus-infected plants, is analysed [81]. On this issue, the phytovirus vectors fitness is also considered, taking into account their infectious state towards their natural enemies. For example, de Oliveira and colleagues [82] noted that *R. padi* carrying CYDV were more vulnerable to the parasitoid wasps *Aphidius colemani* Viereck. Indeed, they experienced higher rates of parasitism, higher overall population suppression and were accepted as hosts by wasps more often compared to non-viruliferous aphids.

With regard to our interest in this review, several studies had analysed the impact of beneficial macroorganisms presence on the behaviour of their hosts, vectors of phytoviruses with an impact on virus spread. Shifting or dispersal are the most important aphid behaviours induced by beneficial macroorganisms presence with a considerable impact on phytoviruses spread. Then, Long and Finke [83] reported that generalist insect predators induced a larger vector movement from plant-to-plant reducing C/BYDV prevalence. Similarly, the spread of CABYV was significantly limited following the increased movement of its *A. gossypii* vector in the presence of the parasitoid *A. colemani* [8]. Additionally, as discussed in Section 2.3, aphid DB impedes the spread of circulative phytoviruses, but may be favourable to non-circulative phytoviruses spread. Indeed, in the same study, Dáder and colleagues [8] found also a significant increase in the spread of CMV transmitted by the same vector, *A. gossypii*. Similarly, Hodge and Powell [24] noted that the presence of *A. ervi* larvae induced a rapid drop off to parasitised *A. pisum* from bean plants and disperse to new hosts. This resulted in a considerably higher infection rate of PEMV (70%) compared to control (25%). It should also be noted that *A. pisum* parasitism by *A. ervi* did not affect the aphid vector efficiency to transmit PEMV. However, this reduced the vector longevity that ultimately led to shorten duration for viruliferous aphids to inoculate virus to plants.

5.1.2. Microorganisms

Most of microorganisms integrated in plant–insect–phytovirus interactions were integrated for experimental purpose. *Hamiltonella defensa* and *Arsenophonus sp.* aphid bacterial endosymbiont differentially influenced the FB (exploratory intracellular puncture) of four clones of *A. craccivora* on infected *C. pepo* with the possibility to enhance acquisition-transmission rates of WMV [54]. Focusing on viruses, Mulot and colleagues [2] provided in vivo evidence for the involvement of membrane-bound Ephrin receptor (Eph) in the transmission of TuYV by *M. persicae* through the in planta- or in vitro-synthesised double-stranded RNA virus (dsRNA) targeting Eph-mRNA ($dsRNA_{Eph}$) in *M. persicae*. There was also *pepper cryptic virus 1* (PCV-1; family Partitiviridae) a latent phytovirus infecting almost all Jalapeño peppers (*Capsicum annuum* L.) [4]. When coinfected with acute phytovirus CMV, PCV-1 indirectly manipulated the HSB of *M. persicae* following altered odour profile of *C. annuum* [4].

More common in the field are cases of co-infection between two phytopathogenic agents. Dos Santos and colleagues [20] studied the impact of co-infection of wheat with *Giberella zeae* (Schwein.) Petch and BYDV on the behaviour and performance of *R. padi*. They found no interference in HSB of viruliferous *R. padi* but they reported 42% population growth on co-infected *Triticum aestivum* L. compared to the control [20]. Furthermore, entomopathogenic fungi are widely used in crop protection. They are rarely integrated into phytovirus pathosystems with the aim of studying their impact on the VTE of aphids. To this end, González-Mas and colleagues [84] reported a modification of several FB parameters of *A. gossypii*, which, however, were not relevant to the phases related to the phytovirus inoculation process.

5.2. Biochemical Components

Some substances biosynthesised by insects or plants in a specific context can be isolated or synthesised for research purposes. For example, (E)-β-farnesene (EβF) is a VOC that serves as an alarm pheromone in numerous aphid species. It is released in response

to a predator attack, inducing dispersal behaviour in conspecifics [85]. Lin and colleagues [12] demonstrated that EβF release induced the dispersal of *M. persicae* and *M. euphorbiae* influencing the spread of phytoviruses under laboratory conditions.

5.3. Chemical and Physical Components

Physico-chemical factors, sometimes related to environmental characteristics, are of great importance. Impacts on plant growth, but also on relationships in phytovirus pathosystems, are dependent on soil factors such as salinity which negatively influenced the aphid population size, altered the soybean VOC and reduced the relative level of soybean mosaic virus (SMV) in aphid-infested plants. Incidence of SMV was dependent on salt-stressed fields [86]. Similarly, water stress (including drought and flooding) conditions altered the vector FB and the accumulation of phytoviruses in vectors' organisms by modulating plant quality (phloem amino acid availability and defence expression). This resulted in the disruption of the vector performance and phytovirus transmission efficiency in TuYV- [1], cauliflower mosaic virus (CaMV)-, turnip mosaic virus (TuMV) [58] and SMV- [87] pathosystems.

In the current context of climate change, del Toro and colleagues [88] recently provided insight into the potential impact of elevated temperature and CO_2 concentration in the atmosphere on the spread of phytoviruses. The probability of transmission of phytovirus by a vector reduced as the virus titers in the donor leaves under elevated temperature and CO_2 concentration conditions. Finally, chemical insecticides used against phytovirus vectors, notably synthetic chemicals, but also essential oils, would have consequences on the propagation of phytoviruses by acting directly on insect behaviour, or indirectly as an elicitor of the plant's immune defence. For example, flonicamid and sulfoxaflor, both systemic insecticides, reduced the percentage of probing time spent in the E2 phase of *M. persicae* exposed to treated *Physallis floridana* Rydb., but induced a higher percentage of probing time spent in the C and F phases compared to the control [48]. Additionally, Vazyl-Y mineral oil spray elicited potato's immune defence system and significantly reduced the infection rate on treated leaves compared to control [89].

6. Concluding Remarks

This review aimed to analyse the aphid behaviour and factors in relation to phytovirus spread with following conclusions to be retained:

- There are two main levels in phytovirus transmission process related to vector mobility and efficiency. The first includes the activities that allow the vector to reach its host plant and the site of phytovirus inoculation. Second concerns the vector capacity to transmit phytovirus to this host plant.
- Host-seeking is the first vector behaviour associated with phytovirus spread. It occurs in successive phases until final acceptance in relation to plant quality leading to sustainable sap ingestion from the host plant.
- Aphid life history performances with subsequent virus transmission efficiency are associated to variable nutrient content quality and the presence/absence of toxins and feeding deterrents.
- Vectorial transmission efficiency refers both to specific vector–phytovirus relationships and environmental conditions.
- All the aphid behaviours developed above could be manipulated by phytoviruses either directly by influencing their vectors or indirectly via their host plants in order to enhance their spread.
- Biological agents including microbial entomopathogens to control aphids are rarely integrated into phytovirus pathosystems even if significant impacts start to be observed.

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