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APHID FEEDING ON PLANT LECTINS FALLING VIRUS TRANSMISSION RATES : A MULTICASE STUDY

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ABSTRACT :

Aphids are insect vectors that have piercing-sucking mouthparts supporting diversified patterns of virus-vector interactions. Aphids primarily retain circulative viruses in the midgut/hindgut, whereas noncirculative viruses tend to be retained in the stylet. Most viruses, and many proteins from animals, have carbohydrate or carbohydrate-binding sites. Lectins vary in their specificity, of which some are able to bind to viral glycoproteins. To assess the potential competition between lectins and viral particles in virus transmission by aphids, this study examined how feeding plant lectins to aphids affects the transmission efficiency of viruses. *Sitobion avenae* (F, 1794) (Homoptera: Aphididae) aphids fed with *Pisum sativum* lectin (PSL) transmitted *Barley yellow dwarf virus* with significantly lower efficiency (four-fold ratio). *Pea enation mosaic virus* was significantly reduced in *Acyrthosiphon pisum* Harris (Homoptera: Aphididae) aphids fed with the lectin Concanavalin A. In comparison, the transmission of *Potato virus* Y was significantly reduced when *Myzus persicae* Sultzer (Homoptera: Aphididae) aphids were fed with PSL.Thus, lectin could be used as a blocking agent of plant viruses, facilitating an alternative approach for crop protection.

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The majority of plant viruses are transmitted by Hemipteran insect vectors, nearly 350 virus species, to a broad range of host plants (Hogenhout et al. 2008). Aphids are the largest models of sucking insects supporting diverse patterns of virus-vector interactions (Blanc et al. 2014). Circulative transmission is transferred to the insect vector by successive steps, from crossing the gut barrier to invading the hemolymph, to reach the salivary glands, after which the virus is transferred to subsequent plants via the saliva of aphids. In comparison, the noncirculative transmission occurs when the virus binding to the insect vector mouthparts and then being released to the plant during feeding. Sophisticated and specific processes are in-volved in both methods of transmission (Blanc et al. 2011). Indeed, although circulative viruses are mainly retained in the midgut/hindgut (Nault and Ammar 1989), noncirculative viruses are mainly retained in the stylet (food canal; Ammar et al. 1994). Naturally, most viruses from animals have either carbohydrate or carbohydrate-binding sites on their surface. These sites bind monosaccharides and oligosaccharides with high specificity. Oligosaccharides are involved in cell adhesion and the recognition of pathogens (Becker et al. 1976).

In the last 25 yr, there has been much interest in the potential of lectins as a form of crop protection. The term 'lectin' was coined by Boyd and Shapleigh in 1954. It originates from the Latin word 'legere', which means 'to select' or 'to bind'. Today, it is used for proteins of nonimmune origin that have at least one noncatalytic domain that specifically and reversibly binds to mono- or oligosaccharides (Carlini and Grossi-de-Sá 2002, Chandra et al. 2006). The molecular structure and specificity of lectins are subject to variation (Peumans and Van Damme 1995). Lectins largely occur in plants, animals, and microorganisms with a wide distribution in nature. They display different roles and functions in many biological processes: from molecule recognition in relation to immune responses in animals (Kilpatrick 2002) to plant defense mechanisms to cope with pests and pathogens (Peumans and Van Damme 1995; Trigueros et al. 2003). The adverse impact of several lectins on insect pests has been demonstrated, with their anti-insect activity increasing the mortality or delaying the development of insects (Sauvion et al. 2004, Francis et al. 2011). The toxic and insecticidal activity of plant lectins (reduced weight and size, developmental delay, mortality, inhibition of nutrition, and reduced fertility) means that they could potentially be used as biopesticides (Habibi et al. 2000, Carlini and Grossi-de-Sá 2002). Insecticidal lectins bind to midgut epithelial cells in a variety of pest species (Habibi et al. 2000). At the cellular level, they act differently on various insect species because they exhibit extremely specific binding to oligosaccharides (Fitches et al. 2001, Sauvion et al. 2004). Moreover, some lectins bind to several pathogens, like viral glycoproteins. These lectins could potentially reduce binding to phytoviruses with receptors located in the stylet or gut of the insect (Naidu et al. 2004). Particular interactions and binding to these receptors with viral glycoproteins could reduce viral transmission (Tang et al. 2015).

To assess the potential competition of lectins toward viral particles in virus transmission by aphids, this study examined how virus transmission efficiency was affected by feeding aphids with three plant lectins with diverse sugar affinity. A multicase study, focusing on both circulative and noncirculative aphid-virus models, with economic importance was used and expected to provide baseline information for developing ways in which lectins can be used to control viral disease in several crops.

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Materials and Methods

APHIDS AND VIRUS ISOLATES

All aphid populations were separately maintained in a climate-controlled room (16 h light; 20 ± 2°C; 70% relative humidity [RH]). English grain aphid, *Sitobion avenae* (Fabricus) clone Shanxi Taiyuan, was reared on wheat (*Triticum aestivum* L. cv. *Toison d'or*), whereas the pea aphid, *Acyrthosiphon pisum* Harris clone YR2, and *Myzus persicae*, clone Gembloux, were reared on broad bean (*Vicia faba* L., 'grosse ordinaire' variety) and tobacco (*Nicotiana tabacum* cv. Xantii), respectively.

Barley yellow dwarf virus (BYDV-PAV) was provided by the Centre Wallon de Recherches Agronomiques (CRA-W). BYDV was maintained by serial aphid transmissions on *T. aestivum. Pea enation mosaic virus* (PEMV) and *Potato virus Y* (PVY) were commercial strains (DSMZ, Braunschweig, Germany) inoculated mechanically to broad bean and tobacco plants, respectively. PEMV and PVY inoculum was prepared according to a similar protocol. Specifically, inoculation buffer (0.05 M sodium/potassium phosphate buffer, pH 7.0; 1 mM ethylenediaminetetraacetic acid; 5 mM diethyldithiocarbamic acid; 5 mM thioglycolic acid) was added to PEMV- or PVY-infected dried plant material (DSMZ or Agdia-Biofords, Evry, France).

ASSAYS OF VIRUS TRANSMISSION EFFICIENCY

To standardize artificial diet experiments, first-instar nymphs (aged 0-24 h) were selected at the onset of each experiment. All assays were carried out independently at different times in a climate-controlled room (16 h light; 20 ± 2°C; 70% RH). A global procedure was used (Fig. 1). Aphids were fed an artificial diet, including 50 µg/ ml *Phaseolus vulgaris* lectin (PHA), Concavalin A (ConA), or *Pisum sativum* lectin (PSL; Sigma-Aldrich, St. Louis, MO) in 15% su-crose solution through a parafilm membrane (two layers of parafilm enclosing 200 µl of diet matter) for 48 h (named PHA-diet/ConA-diet or PSL-diet). The applied lectin concentration was selected due to it having a nontoxic effect on aphids based on previous tests in comparison to a control diet (less than 15% mortality and similar to control diet levels). The lectin-free artificial diet was used as the negative control. These lectins were selected due to their different sugar affinities on cultivated plants (*Phaseolus* or *Pisum*) and commercial availability.

After 2 d of feeding on lectin diet, the aphids were carefully transferred to the new artificial diet containing virus (BYDV for *S. avenae*; PEMV for *A. pisum*; and PVY for *M. persicae*) infected tissues crushed in 15% sucrose. After an acquisition period of 48 h, individual aphids were transferred (one by plant) to wheat (for *S. avenae*), broad bean (for *A. pisum*), or tobacco (for *M. persicae*) plants for a 5-d inoculation access feeding period for BYDV and PEMV, and 30 min for PVY. Three weeks after inoculation, leaf samples were collected and tested for the presence of BYDV, PEMV, and PVY by ELISA based on the manufacturer's instructions (DSMZ or Agdia-Biofords).

Tests were repeated four times with 25 plant replicates each containing one aphid were performed (total: 100 plants per treatment). The influence of lectins on virus transmission (number of virus

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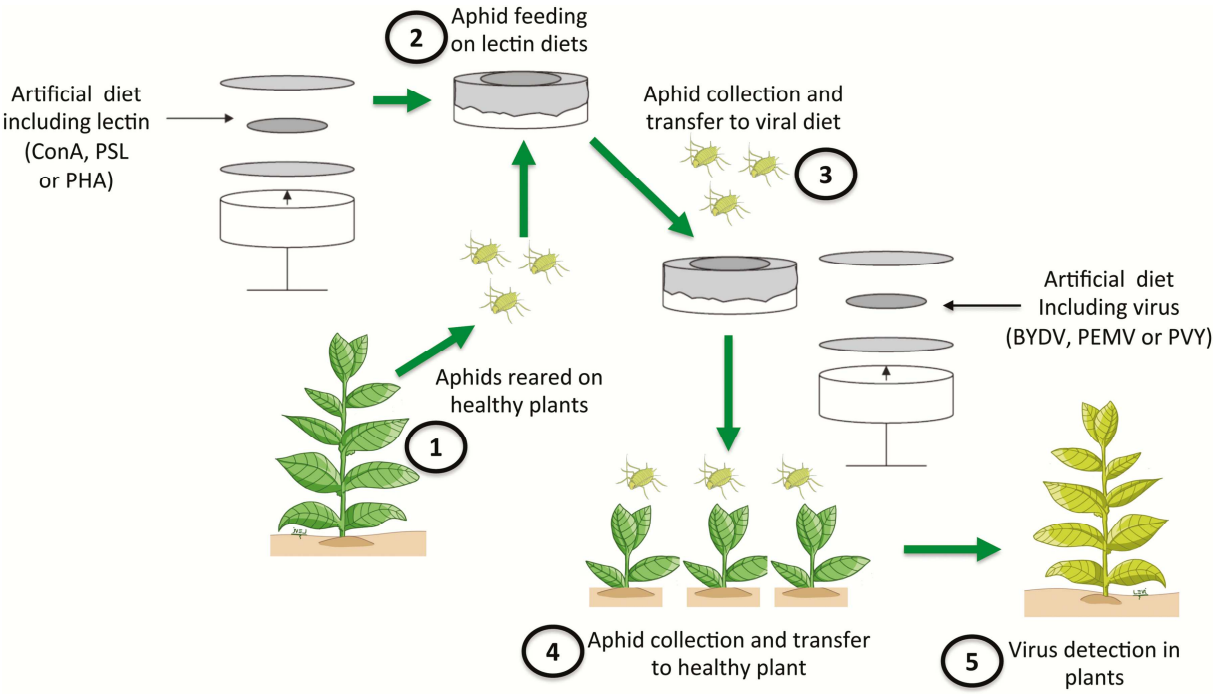
infected plants by batch of plants) was determined with ANOVA analysis after arcsin $\sqrt{x}$ transformation (where x was the virus transmission rate in percent) and mean comparison tests using Minitab software (Minitab 17, State College, Pennsylvania).

***Figure 1**. Illustration of the successive steps of the experimental set-up to investigate how lectin interacts with the transmission of viruses by aphids. BYDV, PEMV, and PVY for Barley yellow dwarf virus, Pea enation mosaic virus, and Potato virus Y, respectively. ConA, PSL, and PHA for Concavalin A lectin, Pisum sativum lectin, and Phaseolus vulgaris lectin, respectively.*



Results

When compared with the control, all three lectins were tested for their impact on BYDV transmission (Fig. 2A). *Sitobion avenae* fed with *Pisum sativum* lectin (PSL) transmitted the virus with significantly lower efficiency (four-fold ratio) compared with the control ($F = 10.63$; df = 3, 15; $P = 0.001$). Reduced but nonsignificant virus transmissions were detected for aphids fed with *Phaseolus agglutinin* (PHA) and Concanavalin A (ConA) compared with the control ($t = 2.08$ and $P = 0.214$ vs $t = 2.19$ and $P = 0.182$, respectively).

PEMV was significantly lower in aphids fed with ConA compared with the control and the two other lectin treatments ($F = 17.04$, df = 3, 15; $P < 0.001$; Fig. 2B). No significant PEMV transmission rates were obtained with aphids that were fed PSL and PHA (t = -0.73, P = 0.883 and t = -2.57, P = 0.099, respectively).

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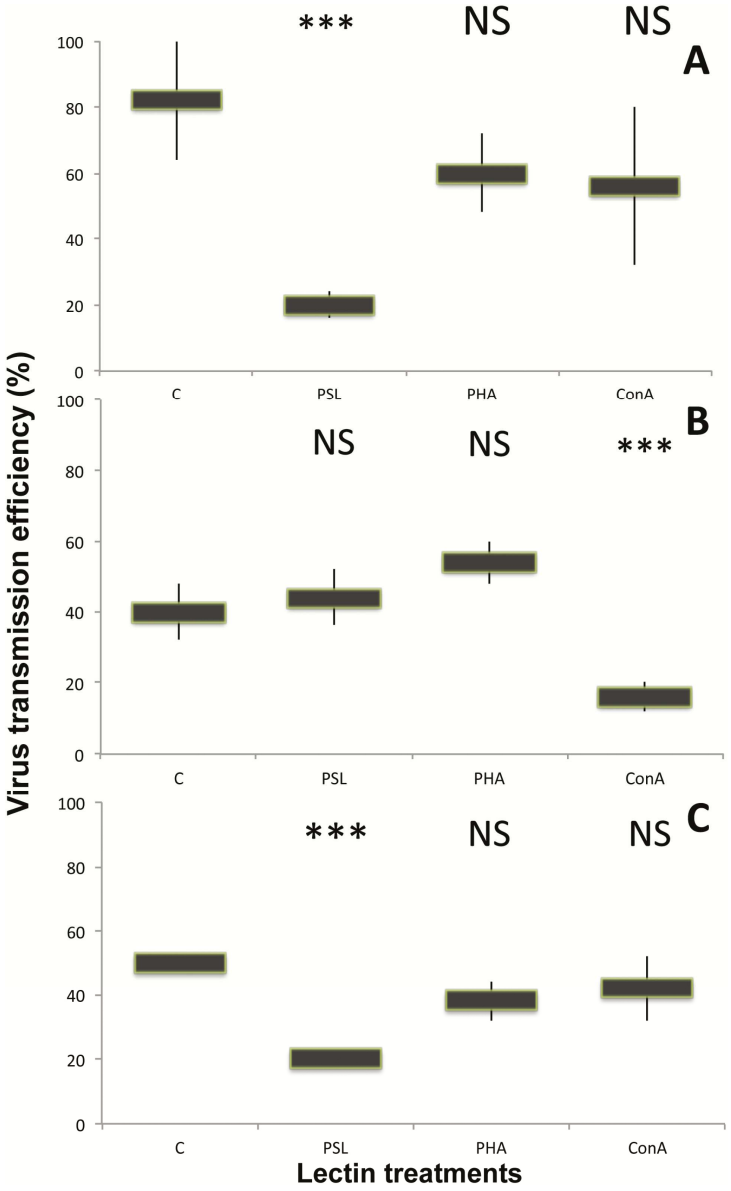
When switching to the noncirculative aphid-virus model (Fig. 2C), *M. persicae* fed with PSL was significantly less efficient at transmitting PVY to plants (with a 2.5-fold ratio reduction; $F = 24.14$; df = 3, 15; $P < 0.001$). Aphids fed with PHA and ConA showed no significant effects (38.0 ± 8.5% and 42.5 ± 14.1%, respectively, compared with 50.0 ± 2.8% for the control; $t = -0.93$ and $P = 0.641$ vs $t = -1.84$ and $P = 0.304$).

Figure 2. *Comparison of virus transmission efficacy (mean ± SD in %) of aphids fed with lectins in different case studies: Barley yellow dwarf virus (BYDV) transmitted by Sitobion avenae (A), Pea enation mosaic virus (PEMV) transmitted by Acyrthosiphon pisum (B), and Potato virus Y(PVY) transmitted by Myzus persicae (C). Treatments were a control (C), Pisum sativum lectin (PSL), Phaseolus agglutinin (PHA), and Concanavalin A lectin (ConA). ***Very highly significant differences at P < 0.001; NS means no significance.*



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Discussion

Aphids cause serious damage to many crops by directly extracting the nutrients from the plants and by acting as vectors for phytoviruses. The utility of lectins for their direct toxic effect on insect biological parameters has been increasingly explored (Sauvion et al. 2004; Francis et al. 2011); however, they have not been selected as efficient pest management tools because the sufficiently high concentrations required to have an effect on viruses. Knowledge of the potential sugar binding ability of lectins, such as phytohemagglutinin (PHA), on midgut epithelial cells and localization in bugs (Habibi et al. 2000) means that these glycosylated proteins could be utilized as a potential way to disrupt aphid-virus interactions and, hence, the efficiency of viral transmission. To inoculate plants during phloem feeding by aphids during the circulative way of virus transmission, two types of binding on receptors for transcytosis should be considered: 1) when crossing the gut epithelium for release in the hemo-coel and 2) at the accessory salivary glands.

Focusing first on our circulative aphid-virus models, two lectins reduced viral transmission rates 2.5- and 4.0-fold with ConA and PSL for *A. pisum*-PEMV and *S. avenae*-BYDV, respectively. Insect guts consist of a monolayer of epithelial cells that are lined on the lumen side with protruding microvilli, which form a brush border and are covered on the outer side with the basal lamina connected by intercellular junctional complexes (Bergelson 2009). The binding of lectins to gut receptors is, in a way, the settlement of a competing barrier that blocks potential links for the virus. This phenomenon should increase the conventional role of the insect gut microvilli by their acting as a barrier for viral entry and dissemination. The cellular receptors of the microvillar membrane of the gut should reduce receptor availability for virus attachment and entry. Almost all gut microvilli contain cellular receptors for persistent nonpropagative plant viruses, such as luteoviruses, to attach (Blanc et al. 2014, Wang et al. 2014). Some 50-94 kDa proteins isolated from the gut have been identified to specifically interact with viral glycoproteins, even if they were not proved to be functional viral receptors (Kikkert et al. 1998, Bandla et al. 1998, Medeiros et al. 2000). Subsequent studies on aphid and luteovirus interactions lead to the identification of viral proteins, such as CP (Coat Protein of 22 kDa), RT (Read-Through domain), and CPRTD of 35-55 kDa; however, the molecular determinants of related host specificity remain unclear (Mayo and Ziegler-Graff 1996, Miller et al. 2002). More recently, evidence that glycans are involved in the uptake of pathogens by insect vectors has increased. Mannose residues constitute the most abundant glycans in the aphid gut, with mannose-binding lectins targeting glycoprotein receptors being found on the insect gut surface (Rahbé et al. 1995, Fitches et al. 2008). The glycans were hypothesized to be mainly involved in luteovirid-aphid interactions, due to 1) the occurrence of receptor proteins on aphid gut epithelium and 2) the abundance of glycoproteins in the aphid gut (Tang et al. 2015). A gut receptor for PEMV was identified to be aminopeptidase N, according to its high glycosylation and binding to the *Galanthus nivalis* agglutinin plant lectin (Linz et al. 2015). In the current study, ConA lectin reduced the transmission of PEMV by *A. pisum*, with the sugar binding capacity of this lectin explaining this phenomenon. In comparison, another lectin, PSL, was more active at reducing the transmission of BYDV by aphid species, *S. avenae*. The circulative Luteoviridae virus, BYDV, displays a high degree of vector specificity in different aphid species living on Poaceae (Bencharki et al. 2000).

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Pea lectin, PSL, was also efficient in reducing viral transmission in the noncirculative virus-aphid model, namely PVY associated with *M. persicae*. The aphid transmission of PVY occurs in a nonpersistent, noncirculating mode (Kerlan 2006). Thus, this process might be an interaction between the virion and a less specific vector than that used in previously studied circulating viruses, PEMV and BYDV. Even if the noncirculative way of transmitting viruses seems to be more mechanistic, particular receptors in the aphid mouthparts are likely involved. Indeed, the beginning of the structural and functional characterization of the acrostyle (last part of the end of the food duct) was presented by Uzest et al. (2007, 2010). A particular protein receptor for Cauliflower mosaic virus (CaMV) was found at the aphid maxillary stylet extremity. Cuticular proteins with a typical conserved motif, RR2, were identified. Different RR subfamilies are related to a variety of virus-interacting proteins that have been identified (Deshoux et al. 2018).

Because some noncirculative viruses in the genera *Potyvirus* and *Cucumovirus* potentially bind to the stylets in the common duct of aphids, they might also use receptor molecules in the acrostyle (Powell 2005). Evidence for the presence of glycosylated residues on the viral structural proteins was also presented for Potato virus X (Tang et al. 2015). The role of the glycosylated plant virus envelope is well known for tospovirus (tomato spotted wilt virus), which is transmitted by thrips (Whitfield et al. 2005). Yet, receptors were recently identified in aphids that transmit CaMV and turnip yellow virus but were not glycosylated (stylin-01 and stylin-02; the former belongs to a cuticular protein subfamily; Webster et al. 2018; the latter belongs to a membrane-bound Ephrin receptor; Mulot et al. 2018). However, the virus receptors in the aphid mouthparts and gut remain largely unknown.

Here, we demonstrated how certain lectins affect various virusaphid vector-associated models differently. The different effects were directly related to the types of lectins that were selected. The lectins were classified into different groups based on their affinity to different monosaccharides, namely, mannose, galactose, glucose/mannose, *N*-acetyl-d-glucosamine, and *N*-acetyl-d-galactosamine. While *Phaseolus vulgaris* lectin (PHA) exhibits *N*-acetyl-d-galactosamine specificity, both Concavalin A (ConA) and *Pisum sativum* lectin (PSL) exhibit mannose/glucose specific binding, but have different properties. Strong affinity for terminal α-d-mannosyl and α-d- glucosyl residues was found for ConA. The dissociation of the latter into dimers occurred at strong acidic pH in the presence of Ca^{2+} and Mn^{2+} ions. At higher pH, from 5.8 to 7.0, ConA occurs as a tetramer, and it aggregates at pH 7.0 and above. For PSL, a broader range of sugar binding was observed in relation to conservative hydroxyl groups of the d-glucopyranose ring found to be essential for binding to proteins. Compared to ConA, PSL is less sensitive to structural variation of inhibiting carbohydrates (Van Wauwe et al. 1975). For example, in our virus-aphid interactions, PSL and ConA displayed different binding characteristics. Pea lectin only bound to two of the five strains of *Rhizobium leguminosarum*, whereas ConA bound to all strains of *R. leguminosarum*, as well as *Rhizobium phaseoli* and *Rhizobium japonicum*. Because these lectins have similar sugar-binding properties, but different physical properties, differences to the binding characteristics of these lectins to various *Rhizobium* strains indicated both the sugar specificity of the lectin and its physical characteristics influence binding (Wong 1980).

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In conclusion, lectin should be used as a blocking agent for plant viruses, not as an entomotoxic compound, to facilitate alternative approaches of crop protection. However, knowledge remains limited regarding virus receptors in insect vectors; thus, complementary studies are required to determine the functional proteins that are involved in the different virus-aphid models. This requirement represents a major challenge in virus-insect interactions. However, it is now possible to identify cellular receptors on aphid stylets and insect gut microvilli for noncirculative and circulative viruses, respectively, using adapted omics techniques associated with membrane overlay binding assays and co-immuno-precipitation in proteomic approach.

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