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Direct and indirect influences of virus–insect vector–plant interactions on non-circulative, semi-persistent virus transmission

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Plant viruses that are transmitted in a non-circulative, semi-persistent (NCSP) manner have determinants on, and/or accessories to, their capsids that facilitate virion binding to specific retention sites in their insect vectors. Bilateral interactions and interactions occurring at the nexus of all three partners (virus, vector and plant) also contribute to transmission by influencing virus acquisition and inoculation. Vector feeding behavior lies at the core of this trio of virus transmission processes (retention–acquisition–inoculation), but transmission may also be mediated by virus infection-triggered and/or vector feeding-triggered plant cues that influence behavioral responses such as vector attraction, deterrence and dispersal. Insights into the multiphasic interactions and coordinated processes will lead to a better understanding of the mechanisms of NCSP transmission.

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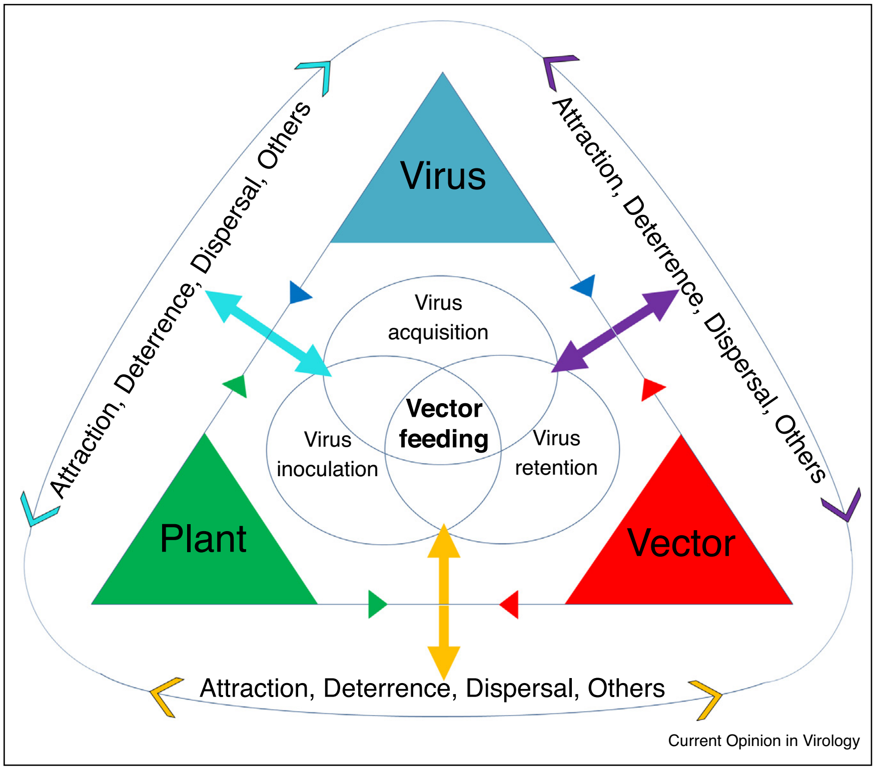
Introduction

In the battle with their hosts, viruses maintain the delicate balance essential to surviving in a hostile environment with depleting finite resources by escaping into new territories through various avenues of transmission. Animal viruses can be transmitted by contact, through bodily fluids and aerosols, and by animal bites such as those taken during a blood meal by hematophagous arthropod vectors of arboviruses [1,2]. In the case of plant viruses, arthropod transmission is accomplished by phytophagous (plant-feeding) vectors, with those in the order Hemiptera, for example, aphids, whiteflies, soft scales, mealybugs, leafhoppers, planthoppers, and treehoppers, being the most significant [3]. Feeding in phytophagous hemipteran insects is facilitated by the piercing action of an elongated bundle of stylets that is capable of weaving between and around cells and sucking up nutrient-rich phloem sap. The vector transmission mechanisms of many plant viruses remain poorly understood. However, it is evident that vector feeding is at the core of, and concomitant with, an ensemble of inter-related virus transmission processes (Figure 1) — first, virus acquisition (acquisition feeding), the process by which a vector ingests sap or fluid from an infected plant, resulting in virus uptake, second, virus transit through and retention (binding) or propagation at specific sites within the vector as ingested sap courses through its digestive system, and third, virus inoculation (inoculation feeding), the process by which a vector egests (regurgitates) ingested fluids or salivates, resulting in the delivery of virus into a recipient plant.

Several modes of virus transmission exist, determined by the characteristics of the transmission processes and, to some extent, tissue tropism, a phenomenon where specific plant tissues preferentially support the proliferation of a virus. The different modes of virus transmission have been well summarized in several recent reviews [4,5]. Here, we focus on non-circulative, semi-persistent (NCSP) transmission, accompanied by references to non-circulative, non-persistent (NCNP) and circulative, non-propagative (CNP) transmission. NCNP viruses tend to infect all cell types and can be acquired from an infected plant and delivered to a recipient plant following a short acquisition access period (AAP) and a short inoculation access period (IAP), respectively (accomplished all within seconds to minutes). They are retained for short durations, losing transmissibility when the vector molts; and virus circulation (transit) through the vector is not a requirement for transmission. CNP viruses tend to exhibit phloem tropism and are acquired from and delivered to the phloem following long (hours to days) AAPs and IAPs, respectively. They are retained for long durations, often over their vectors' entire lifetime, and must circulate through their vectors before they are inoculated into recipient plants. NCSP viruses bare features resembling those of NCNP and CNP viruses — circulation through the vector is not a criterion for transmission, although they tend to, albeit not always, exhibit phloem tropism [6], and transmission is typically associated with long AAPs and IAPs. In addition, their

Figure 1



Direct and indirect influences of virus–vector–plant interactions on NCSP transmission. Viruses achieve transmission by interacting directly with their insect vectors and benefitting from their feeding behaviors/activities (vector feeding) via a continuum of three inter-related transmission processes — acquisition, retention and inoculation (represented by three overlapping circles). Virus (blue), vector (red), and plant (green) undergo bilateral interactions (represented by the two arrow heads, color-coded to match the interacting partners, facing each other on all three sides of the triangle) and trilateral interactions involving all three partners (represented by the entire triangle) to influence various aspects of the transmission processes (represented by the cyan, gold and purple arrows directed at the points of intersection of the three overlapping circles). Bi-lateral and trilateral interactions can also trigger plant cues and/or vector responses that indirectly influence virus transmission by eliciting specific vector responses that is, attraction, deterrence and dispersal (indicated outside the triangle). Specific virus and/or vector triggered plant resistance/defense responses may also indirectly influence virus transmission by targeting/inhibiting the virus and/or the vector (indicated as 'others' outside the triangle).

retention periods are longer than those of NCNP viruses (hours to days), although their transmissibility is also lost upon vector molting.

Depending on the virus–vector–plant combination, the interplay of biological, biochemical and molecular determinants occurring/present in the virus, vector and plant, or at the nexus of their interactions, plays a significant role in determining the success or failure of virus transmission. In this review, we aim to use both a viral-centric and vectorial-centric approach to provide a perspective on what is currently known about the determinants/factors that directly or indirectly influence NCSP transmission.

Direct influences on NCSP virus transmission

Viral determinants mediating virion retention and acquisition

Extensive research with specific NCNP viruses had paved the way for studies on NCSP transmission. Early studies were focused on demonstrating the role of the virion capsid as an important determinant of vector transmission for NCNP viruses (Reviewed in [7]). Out of this requirement for the capsid to mediate virus transmission came the coining of the term 'capsid strategy of transmission'. A more profound deviant of the 'capsid' strategy is the 'helper' strategy, in which virus transmission is mediated by not only the capsid, but also additional viral encoded, non-capsid proteins. We now know that both strategies are involved in mediating the binding of virions to specific retention sites in the insect vectors (Figure 2) (see below).

Fewer NCSP viruses have been described compared to NCNP viruses and detailed knowledge on the mechanism of transmission for many NCSP viruses is still lacking [6]. However, viral determinants and virus–vector interactions mediating NCSP transmission are increasingly being investigated, and we know much more about