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Current Opinion in Insect Science

# Manipulation of hosts and vectors by plant viruses and impact of the environment

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The effect of environmental factors on the efficiency of plant virus transmission is extremely difficult to predict, because they obviously impact concomitantly multiple steps of the complex three-way plant–virus–vector interaction. This review summarizes the diversity of the relationship between plants, viruses and insect vectors, and highlights the numerous phases of this process that can be altered by the virus in ways that can potentially enhance its transmission success. Many of the reported cases are often considered to be possible viral manipulations acting through modifications of the physiology of the host plant, indirectly reaching to the insect vector. Plants are extremely responsive to environmental fluctuations and so interferences with these putative viral manipulations are highly expected. The role of environmental factors in plant virus transmission can thus be envisaged solely in the context of this complexity. It is only briefly evoked here because this field of research is in its infancy and currently suffers from an impressive lack of experimental data.

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**Current Opinion in Insect Science** 2016, **16**:36–43

This review comes from a themed issue on **Vectors and medical and veterinary entomology**

Edited by **Zach N Adelman** and **Kevin Myles**

For a complete overview see the Issue and the Editorial

Available online 13th May 2016

**http://dx.doi.org/10.1016/j.cois.2016.05.007**



## Introduction

As opposed to animals, the immense majority of plants are incapable to move away from any sudden or gradual change of their environment, nor from attacks by herbivores and pathogens. Consequently, plants have developed a large panel of constitutive or inducible protections, defenses, or more generally phenotypic plasticity, to confront and accommodate such changes. A corollary of this fact is that plants have also evolved a very sophisticated arsenal of sensory/perception systems in order to monitor all environmental periodic fluctuations and unpredictable 'anomalies' including abiotic and biotic stresses. This sophistication in plant sensory potential allows timely, diverse and specifically adapted physiological responses and, in some instances, their communication to neighbor plants via volatile emission or information transfer through soil microorganisms [1–3].

In the three-way interaction between a plant, a virus and its insect vector, one must bear in mind that both viral infection and vector feeding will rapidly induce dramatic changes in plant physiology, defensive or not, and that changes induced by viruses and vectors can either be independent, synergistic or antagonistic. The possibility for a virus to antagonize or assist the feeding, settling and development of its vector on their common host is opening the way for possible manipulations, which can ultimately potentiate transmission [4••,5,6•].

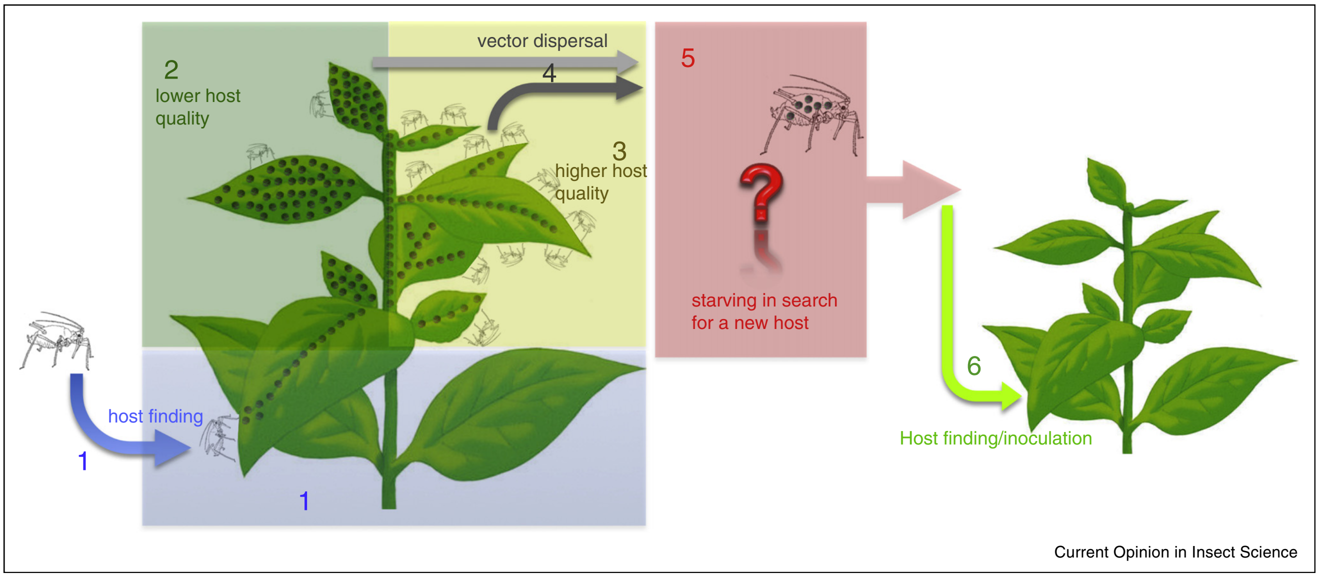
Many plant responses to biotic and abiotic stresses are interconnected [7]. Hence, when environmental factors impact on plant physiology they concomitantly interfere with plant–virus and/or plant–vector relationships and thus with the potential mechanisms by which a virus could manipulate both its host and its vector. The primary scope of this review is to summarize the different modes of vector-transmission of plant viruses [8,9], with a dedicated attention to virus-induced changes in plants and vectors that potentially increase transmission (Figure 1). Though of obvious importance, how environmental factors can modulate these changes and interfere with virus transmission is only briefly evoked because of the paucity of data in the current literature.

## Different modes of insect-transmission by plant viruses

Plant viruses are transmitted by fungi, nematodes, mites, and insects [10], but insects are the only vectors for which sufficient knowledge is available on the complex interactions reviewed in this chapter.

There are few but important distinctions in the mechanisms of interaction between insect vectors and viruses of animals versus plants [11,12]. The first one is that the majority of animal arboviruses actually infect (and thus replicate in) their vectors, whereas most plant viruses do not. In fact, a minority of plant viruses, designated 'circulative propagative' and belonging to families whose members may infect either plants or animals (*Rhabdoviridae*, *Reoviridae*, *Bunyaviridae*), replicate in their insect vectors (Figure 2). These are thought to derive from insect viruses that have secondarily acquired the capacity

**Figure 1**




Steps in the virus transmission process affected by virus and/or the environment. This figure depicts all steps of a plant virus life cycle where the virus can affect both the host plant and the insect vectors in ways that can potentially increase transmission. 1 (lower blue arrow and rectangle): Insect vectors, here aphids, are attracted to infected plants by visual and olfactory cues. 2 (left upper green rectangle): For non-circulative viruses, the quality of the host plant can be decreased by the infection. The insect vectors rapidly acquire the virus from superficial tissues and soon leave in search for a healthy plant (light gray arrow 4). 3 (yellow upper rectangle): For circulative viruses, the quality of the host plant can be improved by the infection. The insect vectors settle, feed from deep tissues, and ingest the virus. The vector population growth is accelerated, leading to overcrowding and increased emigration in search for new host plants (dark gray arrow 4). 5 (red rectangle): This step is the journey of the viruliferous insect vectors away from any host plant. If the vector fails to find a new host, it will die together with the viruses it carries. Viruses could manipulate the motility or survival time of the insect vectors when away from any host. 6 (green arrow): contrary to the preference of virus-free vectors for infected plants (1), virus-loaded vectors are sometimes better attracted by healthy plants. Environmental factors could modify this scheme at any steps in unpredictable ways.

to replicate in and infect plants [11,13,14]. In these cases, insect vectors can be aphids, hoppers, and thrips, and their vector capacity and/or competence is conceptually identical to that amply studied for arboviruses of animals, discussed in [11,14,15].

A second marked distinction is that the 'circulative non-propagative' transmission is frequent and well characterized in plant but not reported in animal viruses [12]. All member species of the families *Luteoviridae*, *Nanoviridae* and *Geminiviridae* traverse the gut of their respective vectors to reach the hemolymph and diffuse to the salivary glands, with no detectable replication (Figure 2), except perhaps for one geminivirus species discussed in [16]. Circulative non-propagative transmission has been reported for vectors such as aphids, whiteflies, and hoppers where viruses accumulate exclusively in gut and salivary gland cells and appear excluded from any other organs [9,10,14]. It seems reasonable to assume that the vector capacity/competence, despite the absence of viral replication, is affected by environmental factors, such as temperature for instance, but limited data are available. Some studies unequivocally demonstrate that the efficiency of transmission of nanoviruses, luteoviruses and geminiviruses by aphids and whiteflies is intimately linked to temperature but the underlying mechanisms have rarely been investigated ([17,18] and references within). The influence of environmental factors on the circulative non-propagative transmission is an emerging research area further discussed in the last section.

Finally, a third distinctive category of virus–vector relationship is the so-called non-circulative transmission. This might be compared to the 'mechanical' transmission of animal arboviruses (believed to result from non-specific contamination of biting-insect mouthparts) [12], but in all well studied cases of plant non-circulative viruses, a very specific molecular interaction between unidentified receptors located in the anterior alimentary tract of the vectors and viral ligands has been evidenced. Despite these specific molecular interactions, the contact between non-circulative viruses and their insect vectors is external, limited to the cuticle lining the vectors' mouthparts or foregut [9,19] (Figure 2), and thus it may be anticipated that the virus has little opportunities to significantly directly modify vector behavior or life history traits. A legitimate question is thus whether it is relevant to