

New Synthesis: Investigating Mutualisms in Virus-Vector Interactions

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Most plant viruses depend on insect vectors for transmission from one host to another. Aphids are the most notable among these insect vectors, transmitting more than half of all described virus species. Virus transmission ranges from simple attachment to the tip of the aphid stylets to more complicated interactions that involve ingestion of the viruses, passage through the haemolymph to the salivary glands, and subsequent injection into a new host plant. Plant viruses, which clearly benefit from being transported to new hosts, generally do not harm their aphid vectors. To the contrary, the frequent observation of improved aphid growth on virus-infected plants suggests that these interactions can be mutualistic, benefitting both the viruses and their insect vectors.

Several studies have demonstrated that plant viruses manipulate plants, thus increasing the number of inoculated insect vectors. This can be accomplished by attracting aphids to infected plants and/or changing plant physiology in a manner that improves aphid reproduction. Increased fecundity and developmental rate of aphids on virus-infected plants will result in greater dispersal of viruliferous aphids to new hosts as host plant quality declines and aphids become crowded. Crowding also induces the formation of alate aphids, which provide longer-distance virus transmission. Virus-vector interactions can be mediated indirectly by virus-induced increases in plant nutritive value, suppression of plant defense responses, or some combination of these effects. Recent publications provide evidence for active manipulation of herbivore defenses by plant-pathogenic viruses. For instance, the 2b silencing suppressor protein of cucumber mosaic virus compromises jasmonate-regulated insect defenses and improves performance of *Myzus persicae* (green peach aphid; Lewsey et al. 2010). Similarly, pathogenicity factor β C1, which is encoded in the betasatellite of tomato yellow leaf curl China virus, suppresses jasmonate-mediated defenses and improves growth of *Bemisia tabaci* (silverleaf whitefly) on *Nicotiana tabacum* (Zhang et al. 2012).

Because arthropod-mediated transmission benefits plant viruses, and there is an apparent reproductive benefit for the insects, in many cases, the virus-vector interaction can be considered a mutualism. For instance, individual aphids that transport viruses to a new host plant would benefit from rapid virus-mediated suppression of plant defenses. In such a situation, it clearly would be advantageous for aphids to pick up and transmit viruses. It is also possible that, by transmitting plant-pathogenic

viruses, hemipteran insects can expand their ranges to include normally unsuitable host plants. Our own unpublished observations show that, if *Nicotiana benthamiana* is infected with tumip mosaic virus, the survival of newly arriving *Myzus persicae* (green peach aphids) increases from 30 % to 90 %. Similarly, *N. tabacum* is a poor host for some *B. tabaci* biotypes, but whitefly performance is improved greatly through prior begomovirus infection (Zhang et al. 2012).

If an insect vector arriving at an uninfected plant benefits from being viruliferous, this suggests that such insects will benefit by acquiring viruses prior to moving to new host plants. For instance, aphids could be feeding from virus-infected tissue in a targeted manner, or specifically selecting virus-infected cells as they are probing to reach the phloem. When an aphid punctures a cell infected with cauliflower mosaic virus, the virus rearranges itself rapidly, thereby promoting attachment to the aphid stylets (Martiniere et al. 2013). It has been suggested that this is due to viral recognition of some component of the plant defense signaling pathway that is triggered by aphid feeding. However, it also is possible that the aphids acquire viruses by actively manipulating plant cellular metabolism. Conversely, when a viruliferous aphid settles on a new plant, its feeding success may be promoted if viruses are deposited in a cellular location that allows rapid replication and thereby suppression of plant defenses.

To date, most research on the molecular mechanisms of virus-vector interactions has focused on studying host plant manipulation by viruses that promotes aphid performance. However, aphids and other insect vectors also may promote virus transmission by altering plant physiology. To initiate progress in this research area, it will be necessary to identify conditions under which there are immediate benefits to insect vectors carrying viruses to new host plants. Furthermore, future investigation of these ecologically important but relatively under-investigated three-way interactions should include a greater focus on discovering behavioral and molecular mechanisms by which insect vectors can actively manipulate plant-virus interactions for their own benefit.

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