Effects of *Cucumber mosaic virus* infection on vector and non-vector herbivores of squash

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**Key words:** vector behavior, Cucumber mosaic virus, volatiles, parasite manipulation, *Anasa tristis*, *Cucurbita pepo*

**Abbreviations:** CMV, Cucumber mosaic virus; *A. tristis*, *Anasa tristis*; *C. pepo*, *Cucurbita pepo*

Submitted: 07/20/10

Accepted: 07/20/10

Previously published online: www.landesbioscience.com/journals/cib/article/13094

DOI: 10.4161/cib.3.6.13094

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Plant chemicals mediating interactions with insect herbivores seem a likely target for manipulation by insect-vector plant pathogens. Yet, little is currently known about the chemical ecology of insect-vectored diseases or their effects on the ecology of vector and non-vector insects. We recently reported that a widespread plant pathogen, Cucumber mosaic virus (CMV); greatly reduces the quality of host-plants (squash) for aphid vectors, but that aphids are nevertheless attracted to the odors of infected plants—which exhibit elevated emissions of a volatile blend otherwise similar to the odor of healthy plants. This finding suggests that exaggerating existing host-location cues can be a viable vector attraction strategy for pathogens that otherwise reduce host quality for vectors. Here we report additional data regarding the effects of CMV infection on plant interactions with a common non-vector herbivore, the squash bug, *Anasa tristis*, which is a pest in this system. We found that adult *A. tristis* females preferred to oviposit on healthy plants in the field, and that healthy plants supported higher populations of nymphs. Collectively, our recent findings suggest that CMV-induced changes in host plant chemistry influence the behavior of both vector and non-vector herbivores, with significant implications both for disease spread and for broader community-level interactions.

Because the transmission dynamics of insect-vectored diseases are determined by complex interactions among pathogens, hosts and vectors, the elucidation of these interactions has potentially important implications for human health and agriculture. A number of recent studies have shown that vector-borne pathogens can induce chemical and physical changes in their primary hosts that affect interactions between hosts and vectors, with significant implications for disease transmission. More generally, pathogen effects on host phenotypes have been shown to have broader implications for ecology and ecosystem function—for example by affecting interactions between hosts and other (vector or non-vector) organisms in ways that can modify food webs, alter the outcome of competitive interactions and influence flows of energy and nutrients. In plant systems, only a handful of studies have explored the effects of pathogens on chemically mediated interactions between plants and insects, in contrast to the extensive literature that has examined the effects of herbivore-induced changes in plant chemistry on plant-herbivore-natural enemy interactions.

Recently, we began investigating the effects of a widespread plant pathogen, CMV, on the plant chemistry and chemically mediated ecology of common squash (*Cucurbita pepo*), a frequent host for CMV that also interacts with a variety of aphid vectors and other non-vector insects (Fig. 1). CMV is a widespread and economically important plant antagonist belonging to a class of pathogens—non-persistent viruses—that are particularly difficult to control because they are rapidly transmitted from infected to healthy hosts through brief probes of epidermal plant tissue by aphid vectors. This
transmission mechanism contrasts with that of persistent viruses, which require sustained aphid feeding in the phloem of infected plants for acquisition and are transmitted when an infected aphid again feeds on a susceptible host.10,21 The few previous studies that examined effects of plant viruses on host chemistry and vector behavior focused on persistently transmitted viruses (e.g., Potato leaf roll virus and Barley yellow dwarf virus, two serious agricultural pests) and found a tendency toward enhanced quality of infected plants for aphid vectors—apparently leading to preferential aphid colonization and feeding on infected plants, rapid population growth, and the eventual dispersal of infected aphids to new, healthy, hosts.10,22,23 Consistent with the enhanced quality of infected plants for aphids, previous studies also found that aphids were preferentially attracted to the distinctive odor profiles of CMV-infected plants compared to those of healthy plants, likely because infected plants exhibit greatly elevated emissions of a volatile blend that is otherwise similar to the odor of healthy plants—in contrast to previous findings for persistent viruses, which induced characteristic odor profiles.5,9,13 Thus, CMV-infected plants may be attractive to aphid vectors because they mimic the odors of large, healthy plants.

While too few systems have been explored to draw broad conclusions, the contrast between our findings for CMV and those previously reported for persistent viruses suggest that transmission mechanism may be an important factor shaping pathogen effects on host plant phenotypes that influence interactions with insect vectors. Although the effects of CMV on host plant chemistry appear to be quite different from those previously reported for persistent viruses, the overall pattern appears conducive to transmission in both cases. Persistent viruses require sustained aphid feeding for transmission and appear to induce plant phenotypes that attract and then arrest aphids, while CMV, which like other non-persistent viruses benefits from frequent aphid movement among plants, induces a phenotype that attracts aphids then causes rapid dispersal. The potential generality of this pattern is supported by work on other non-persistent viruses demonstrating similar reductions in plant quality for aphid vectors.25,26

In addition to the implications for disease transmission discussed above, pathogen-induced changes in plant phenotypes can have important impacts on ecological interactions with other, non-vector insects. For example, infection can alter plant nutritional quality and defense status (e.g., levels of secondary compounds or the induction of defense-related phytohormones), which can influence the distribution and abundance of herbivores feeding on a given plant species.27,28 A few studies have documented such effects—for instance, Colorado potato beetles had increased survival on tomato plants infected with Tobacco mosaic virus,29 while local infection of tobacco by the same virus decreased weight gain of tobacco hornworm caterpillars on systemic leaves.30 However, such interactions have rarely been examined under field conditions. Expanding upon our findings regarding the effects of CMV on interactions between squash plants and aphid vectors, we conducted a field study exploring the effects of CMV infection on plant interactions with a common non-vector herbivore, the squash bug (Anasa tristis; Fig. 1E and F).
Squash bugs are important agricultural pests that feed exclusively on plants in the Cucurbitaceae family, and our study plant (C. pepo) is a preferred host. Throughout the growing season, we tracked colonization of plants by observing egg-laying by A. tristis females and feeding by nymphs on healthy and infected plants. We observed that adult squash bugs laid eggs on healthy squash plants in preference to infected plants (Fig. 2). As a consequence of this preference there were fewer nymphs on infected squash plants once eggs began hatching (Fig. 3). Although we did not directly assess developmental rates or survival of nymphs on infected and healthy plants, the clear oviposition preference for healthy plants exhibited by A. tristis females suggests that the negative impacts of CMV infection on host plant phenotypes—which may be shaped by their implications for transmission by insect vectors—can also have significant impacts on plant interactions with non-vector herbivores, with implications for community structure and dynamics.

Our recent findings, and those reported here, suggest that transmission mechanism is a major factor shaping the effects of plant viruses (and potentially other pathogens) on host plant phenotypes, and that these effects can have significant impacts on plant interactions with both vector and non-vector insects. Future work in this system will focus on elucidating the mechanisms underlying the observed effects of CMV on host plant quality for insect herbivores and further exploring the consequences of these effects for community- and landscape-level ecological interactions.

Acknowledgements

The pathogen CMV-FNY was kindly provided by Dr. John Murphy (Auburn University). We thank F.E. Gildow for assistance in developing the inoculation protocols; and J.C. Saunders and E. Smyers for technical assistance. Funding for this research was provided by a grant (2008-35302-04577) from the U.S. Department of Agriculture’s National Research Initiative and by a Doctoral Dissertation Improvement Grant (DEB-1011122) from the National Science Foundation.

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