Transmission of Grapevine Red Blotch Virus: A Virologist’s Perspective of the Literature and a Few Recommendations

Madison Flasco 1, Victoria Hoyle 1, Elizabeth J. Cieniewicz 2, and Marc Fuchs 1*

1Cornell University, School of Integrative Plant Science, Plant Pathology and Plant-Microbe Biology, Geneva, NY 14456;  2 Plant and Environmental Sciences, Clemson University, Clemson, SC 29634.

*Corresponding author (mf13@cornell.edu; Tel: 315 787 2487; Fax: 315 789 2389)

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Abstract

Background and goals
Grapevine red blotch virus (GRBV) is the causal agent of red blotch disease, a major threat to grape production and vineyard profitability. Several species of Cicadellidae and Membracidae, including the three-cornered alfalfa hopper (Spissistilus festinus), have been reported to transmit GRBV in the greenhouse, but their capacity to act as vectors in the vineyard remains a source of confusion. This article examines the literature on GRBV transmission and provides recommendations to convincingly identify arthropod vectors.

Methods and key findings
We thoroughly evaluated transmission assays of GRBV that have been reported thus far, and critically analyzed their strengths and limitations. We identified experimental ambiguities and discussed how these have prevented the recognition of S. festinus as a GRBV vector of epidemiological relevance in the vineyard. Based on our assessments and given the circulative transmission mode of GRBV, we formulated a few recommendations to accurately determine how GRBV spreads, and by which insect vectors. These include the testing of the salivary glands of vector candidates for the virus, the determination of an optimal acquisition access period, the use of alfalfa plants for insect gut clearing following the access acquisition period and preceding the inoculation access period, and the inclusion of excised grapevine leaves as virus recipient tissue in transmission assays.

Conclusions and significance
There is a great deal of confusion about how GRBV spreads, and which insect transmits the virus in the vineyard. Our recommendations pertain to the accurate identification of arthropod vectors, which in turn provide an opportunity to address uncertainties relating to GRBV transmission, and will aid in the development of red blotch disease management strategies.

Key words: geminivirus, grapevine red blotch virus, red blotch disease, Spissistilus festinus, three-cornered alfalfa hopper, transmission

Introduction
Red blotch disease is a concern to the grape and wine industries because it delays fruit ripening, reduces fruit quality, and alters wine composition and sensory attributes (Cieniewicz et al. 2017a, Rumbaugh et al. 2021). The estimated economic impact of the disease was found to range from $2213 to $68,548/ha over a 25-year lifespan of a Cabernet Sauvignon vineyard in northern California (Ricketts et al. 2017).

Grapevine red blotch virus (GRBV) is the causal agent of red blotch disease (Yepes et al. 2018). The presence of this virus has been reported throughout the United States (Krenz et al. 2014), Canada (Xiao et al. 2015, Poojari et al. 2017, Fall et al. 2020), and Mexico (Gasperin-Bulbarela et al. 2019). GRBV has also been documented in Switzerland (Reynard et al. 2018), South Korea (Lim et al. 2016), Argentina (Luna et al. 2019), India (Marwal et al. 2019), Italy (Bertazzon et al. 2021), France (Reynard et al. 2022), and Australia (Agriculture Australia 2022). The broad geographic distribution of GRBV is explained by the exchange of infected propagation materials and/or planting stock. Interestingly, GRBV was recently predicted to have originated from a wild Vitis latent virus (Thompson 2022), a closely related virus that is widespread in free-living grapevines in northern California (Cieniewicz et al. 2018b, Perry et al. 2018).

GRBV is a geminivirus with a single-stranded, circular DNA genome that codes bidirectionally for seven open reading frames (Cieniewicz et al. 2017a, Vargas-Asencio et al. 2019). Geminiviruses are categorized into 14 distinct genera based on their phylogenetic relationships, genome organization, and insect vectors (Fiollo-Olivé et al. 2021). These viruses are transmitted in a virus-genus
specific manner by distinct arthropod vectors, including whiteflies (begomoviruses), aphids (capulavirus), treehoppers (grabloviruses, topocuviruses), and leafhoppers (becurtoviruses, curtoviruses, mastreviruses, multiviruses, turnovirus) (Fiallo-Olivé et al. 2021). Insect vectors of citloviruses, eragroviruses, maldoviruses, opunviruses, and topleviruses are currently unknown (Fiallo-Olivé et al. 2021).

The transmission mode of most geminiviruses is circulative (i.e., the virus transits through the body of the insect vector) and nonpropagative (i.e., the virus does not replicate in the insect vector), with common patterns but subtle distinctive attributes and efficiencies (Fiallo-Olivé et al. 2020, 2021). Transmission starts with the insect vector feeding on the phloem sap of infected plants (Figure 1). Then, virions are ingested and travel through the alimentary canal and traverse the gut of the insect vector. Next, virions move across the gut epithelium, likely via transcytosis, circulate in the hemolymph, and then reach the salivary glands (Figure 1). The virions must move through the salivary glands for geminivirus transmission to occur (Blanc et al. 2014, Whitfield et al. 2015, Fiallo-Olivé et al. 2020, Wang and Blanc 2021). After acquisition, the virus is transmissible upon feeding into the phloem of host plants by way of the salivary canal (Figure 1). This process, from ingestion to virus movement in an insect vector, can range from a few minutes to several days, depending on specific interactions between virus and insect proteins, and the virus tissue tropism in the vector body (Whitfield et al. 2015, Wang and Blanc 2021).

Several species of treehoppers (Membracidae) and leafhoppers (Cicadellidae) have been reported to transmit GRBV (Poojari et al. 2013, Bahder et al. 2016, Flasco et al. 2021, 2023a, Kahl et al. 2021, Hoyle et al. 2022, LaFond et al. 2022). However, there is a great deal of confusion about the capacity of some of these insects to transmit GRBV. Hesitancy arose from transmission assays that were not replicated or likely used a suboptimal acquisition access period (AAP) and thus could not be independently validated. Further confusion is explained by the shortcomings of insect surveys performed in red blotch-diseased vineyards, which either failed to consider phloem-feeders as preferred vector candidates or did not recognize how geminiviruses are transmitted by their insect vectors. Additional uncertainty is due to transmission assays that did not use plant material as virus recipient tissue (Table 1). This confusion has hindered the progression of research on the identification of a GRBV vector of epidemiological relevance and, more importantly, has impeded the development of red blotch disease management strategies that resonate with the wine and grape industries. A lack of reliable information on disease ecology has been identified as a major limiting factor for the adoption of red blotch disease management practices by grower communities (Hobbs et al. 2022).

![Figure 1](image-url) Schematic representation of the transmission mode of grapevine red blotch virus (GRBV) by *Spissitilus festinus*. A specimen feeding on the phloem sap of an infected grapevine ingests the virus (blue circles) via the food canal and traverses the gut of the insect. Then, the virus moves across the gut epithelium, circulates in the hemolymph, and reaches the salivary glands. Finally, the virus is transmissible through the salivary canal upon a new feeding event in the phloem sap of a healthy grapevine. Moving through the salivary glands is crucial for GRBV transmission to occur (Flasco et al. 2021). Following exposure to a GRBV-infected grapevine, it takes five, eight, and 10 days for GRBV to be detected in the gut, hemolymph, and head and salivary glands of *S. festinus*, respectively (Flasco et al. 2021).
**Spissistilus festinus is an Epidemiologically Important GRBV Vector**

Based on the genetic relationship of GRBV and other geminiviruses, testing the transmission capacity of treehoppers, including *Spissistilus festinus* (Say), the three-cornered alfalfa hopper, over other insects, is well received (Bahder et al. 2016, Flasco et al. 2021, 2023a, Kahl et al. 2021, Hoyle et al. 2022, LaFond et al. 2022). *S. festinus* is a phloem-feeder reported to transmit GRBV from infected to healthy grapevines in the greenhouse at a rate of 20% in a single experiment performed with a 48-hr AAP (Bahder et al. 2016). The virus was detected in recipient grapevines sourced from a nursery five months postinoculation by the treehoppers (Table 1). Recently, we published a culmination of experiments designed to iteratively characterize the transmission of GRBV by *S. festinus*, particularly the time needed for the virus to be ingested, transit through the insect body, and reach the salivary glands to be transmissible to a healthy plant (Flasco et al. 2021). Multiple experimental replicates yielded consistent results (Table 1). First, the mode of transmission was shown to be circulative and nonpropagative, with a 10-day AAP on infected grapevines (Figure 1) and a six-day AAP on infected snap bean plants, after which the virus was detectable in the salivary glands (Flasco et al. 2021). Consequently, transmission could not be documented if *S. festinus* were exposed for less than 10 days on GRBV-infected grapevines or less than six days on snap beans infected upon delivery of an infectious GRBV clone via *Agrobacterium tumefaciens*-mediated inoculation (Flasco et al. 2021). Transmission of GRBV from infected grapevines to GRBV-free detached grapevine leaves by *S. festinus* occurred at an average rate of 10% (4 of 39) in triplicated experiments carried out in the greenhouse with a 10-day AAP (Flasco et al. 2021). Using snap bean as both donor and recipient material of the virus, the average transmission rate of GRBV by *S. festinus* in triplicated assays was 89% (34 of 38) (Flasco et al. 2021). Independent follow-up experiments with a 10-day AAP revealed a 19% (5 of 27) transmission rate of GRBV by *S. festinus* from infected grapevines to GRBV-free grapevines, and a 77% (10 of 13) transmission rate from infected, free-living grapevines to GRBV-free free-living grapevines in replicated experiments in the greenhouse (Hoyle et al. 2022) (Table 1). Our greenhouse experiments used alfalfa plants, a nonhost of GRBV, for a 48-hr gut clearing of *S. festinus* after the AAP, and excised grapevine leaves or excised snap bean trifoliates as virus recipient tissue (Flasco et al. 2021, Hoyle et al. 2022). Including alfalfa plants in transmission assays increased confidence in the ability of *S. festinus* to acquire, rather than ingest, GRBV upon feeding on infected plants. More importantly, the use of at least a 10-day AAP in controlled release experiments was paramount for documenting the capacity of *S. festinus* to transmit the virus to healthy grapevines in two vineyards, one in California and one in New York, and to acquire GRBV from infected grapevines in a diseased vineyard (Flasco et al. 2023a) (Table 1). Collectively, these findings irrefutably documented this treehopper as a GRBV vector of epidemiological relevance (Flasco et al. 2023a).

**Other Insect Vector Candidates of GRBV**

Beyond *S. festinus*, many treehopper species are present in vineyard ecosystems (Cieniewicz et al. 2019, Dalton et al. 2020, Kahl et al. 2021, LaFond et al. 2022, Wilson et al. 2022), but knowledge on their capacity as vectors of GRBV is scarce. For example, field-caught specimens of keeled treehoppers, *Entylia carinata* and *Enchenopa binotata*, were documented in a single experiment in the greenhouse to transmit GRBV from infected grapevines to GRBV-free grapevines at a rate of 67% (4 of 6) with a 48-hr AAP (LaFond et al. 2022). GRBV was detected in the phloem scrapings but not in the leaf petioles of recipient GRBV-free grapevines after four months of exposure to the treehoppers. This diagnostic result was unexpected, as GRBV is readily detected in leaf petioles and phloem scrapings of systemically infected grapevines (Al Rwahnih et al. 2013, Krenz et al. 2014, DeShield and KC 2023). Nonetheless, the transmission results obtained with *Ent. carinata* and *Ench. binotata* are encouraging, although more work is needed to ascertain their transmission capacity of GRBV.

**Tissue Tropism of the Virus Should Match the Preferred Insect Vector Feeding Site**

The first insect reported to transmit GRBV was *Erythroneura ziczac* (Walsh), the Virginia creeper leafhopper (Poojari et al. 2013). Transmission of GRBV by *E. ziczac* specimens from a colony maintained on grapevine was documented from infected grapevines to GRBV-free grapevines at a rate of 100% (25 of 25) in a single experiment carried out in the greenhouse with a 72-hr AAP (Table 1). Interestingly, the GRBV coat protein (CP) gene sequence is genetically distinct from that of leafhopper-transmitted geminiviruses (Fiallo-Olivé et al. 2021). Therefore, assuming the CP is a major determinant of transmission (Whitfield et al. 2015, Fiallo-Olivé et al. 2020, Wang and Blanc 2021), leafhoppers are unlikely to act as vectors of GRBV, although it should be recognized that these insects are paraphyletic with respect to treehoppers (Dietrich et al. 2017); hence, the existence of a phloem-feeding leafhopper vector cannot be entirely ruled out. Nonetheless, the capacity of the leafhopper *E. ziczac* to transmit GRBV (Poojari et al. 2013) could not be independently confirmed (Bahder et al. 2016, Kahl et al. 2021). Moreover, *E. ziczac* are predominantly mesophyll feeders (Saguez et al. 2015) and GRBV is phloem-limited (Al Rwahnih et al. 2013, Poojari et al. 2013). Such antagonistic features are not expected to yield the 100% transmission rate reported by Poojari et al. (2013). Furthermore, insect surveys in red blotch–diseased vineyards with documented spread did not
Table 1: Summary of published research on grapevine red blotch virus (GRBV) transmission assays utilizing distinct vector candidates.

<table>
<thead>
<tr>
<th>Vector candidate</th>
<th>Preferred tissue of feeding</th>
<th>Donor plant</th>
<th>Recipient plant</th>
<th>AAP(^a)</th>
<th>IAP(^b)</th>
<th>Acquisition (^c)</th>
<th>Transmission (^d)</th>
<th>Experimental replicates (^e)</th>
<th>Number of insects exposed to healthy recipient tissue per biological replicate.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Virginia creeper leaf hopper (Erythroneura ziczac Walsh)</td>
<td>Mesophyll</td>
<td>Reared on grapevines</td>
<td>Grapevines</td>
<td>72 hrs</td>
<td>n.t.</td>
<td>315 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>30-25</td>
</tr>
<tr>
<td>Three-cornered alfalfa hopper (Spissistilus festinus)</td>
<td>Phloem</td>
<td>Reared on alfalfa and snap beans</td>
<td>GRBV-infected grapevines</td>
<td>Detached held free-long grape leaves</td>
<td>48 hrs</td>
<td>48 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>Three-cornered alfalfa hopper (S. festinus)</td>
<td>Phloem</td>
<td>Reared on alfalfa and snap beans</td>
<td>GRBV-infected grapevines</td>
<td>Detached collected phloem</td>
<td>48 hrs</td>
<td>48 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>6-10</td>
</tr>
<tr>
<td>Three-cornered alfalfa hopper (S. festinus)</td>
<td>Phloem</td>
<td>Reared on alfalfa and snap beans</td>
<td>GRBV-infected grapevines</td>
<td>Detached collected phloem</td>
<td>48 hrs</td>
<td>48 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Three-cornered alfalfa hopper (S. festinus)</td>
<td>Phloem</td>
<td>Reared on alfalfa and snap beans</td>
<td>GRBV-infected grapevines</td>
<td>Detached collected phloem</td>
<td>48 hrs</td>
<td>48 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Three-cornered alfalfa hopper (S. festinus)</td>
<td>Phloem</td>
<td>Reared on alfalfa and snap beans</td>
<td>GRBV-infected grapevines</td>
<td>Detached collected phloem</td>
<td>48 hrs</td>
<td>48 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Stictocephala basalis</td>
<td>Phloem</td>
<td>Collected from environment</td>
<td>GRBV-infected grapevines</td>
<td>Artificial sucrose diet</td>
<td>72 hrs</td>
<td>72 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Stictocephala bisonia</td>
<td>Phloem</td>
<td>Collected from environment</td>
<td>GRBV-infected grapevines</td>
<td>Artificial sucrose diet</td>
<td>72 hrs</td>
<td>72 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Entylia carinata</td>
<td>Phloem</td>
<td>Collected from environment</td>
<td>GRBV-infected grapevines</td>
<td>Artificial sucrose diet</td>
<td>72 hrs</td>
<td>72 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Enchenopa binotata</td>
<td>Phloem</td>
<td>Collected from environment</td>
<td>GRBV-infected grapevines</td>
<td>Artificial sucrose diet</td>
<td>72 hrs</td>
<td>72 hrs</td>
<td>n.t.</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

\(^a\) Location insects were collected from, or reared upon, plants in laboratory settings for experimentation.

\(^b\) GRBV-positive plant material used as donor material for transmission experiments.

\(^c\) Tissue in which viruliferous insects fed upon in transmission experiments.

\(^d\) Acquisition access period; period for which vector candidates were allowed to feed upon infected plant tissue.

\(^e\) Transmission access period; period for which vector candidates were allowed to inoculate uninfected plant tissue.

\(^f\) The proportion of tissue testing positive for GRBV after inoculation on recipient tissue is indicated. n.t., not tested.

\(^g\) The number of viral replicates described in the original publication.

\(^h\) Number of viruliferous insects exposed to healthy recipient tissue per biological replicate.
identify E. ziczac as a vector candidate because most Erythroneura specimens that were tested, including E. ziczac, were negative for GRBV via PCR (Cieniewicz et al. 2018a, 2019, Wilson et al. 2022). Finally, E. ziczac are present in many vineyards, sometimes in large populations (Saguez et al. 2014, O’Hearn and Walsh 2017, Wilson 2019). If this leafhopper species was an epidemiologically important vector of GRBV, virus transmission would likely be extensive and homogenous within vineyards. This is not the case, except at the edge of some vineyards where diseased grapevines are aggregated (Cieniewicz et al. 2017b, 2019, Dalton et al. 2019, KC et al. 2022, Flasco et al. 2023b). Overall, the experimental evidence to convincingly support the capacity of E. ziczac or any other leafhopper to act as a vector of GRBV is lacking.

**Experimental Designs May Lead to Artifacts**

The capacity of field-captured specimens of buffalo treehoppers, Stictocephala basalis and Stictocephala bisonia, to transmit GRBV was tested. GRBV DNA was detected in an artificial sucrose solution fed on by viruliferous buffalo treehoppers in a single experiment in the laboratory at a rate of 11% (9 of 82) with a 72-hr AAP, but not from infected grapevines to GRBV-free grapevines (Kahl et al. 2021). The use of an artificial diet is rather peculiar for assessing circulative virus transmission. This is because the presence of viral DNA in the artificial diet following insect feeding may simply be explained by the presence of the virus in the gut or mouthparts of the insects, or the virus being expelled from the insect’s gut as waste material in the form of honeydew, as reported for a whitefly-transmitted geminivirus (Rosell et al. 1999). The use of a non-host plant of GRBV, such as alfalfa (Flasco et al. 2021), would have been helpful for insect gut clearing to differentiate virus ingestion from virus acquisition by ensuring salivary canal-mediated transmission resulting from the transit of the virus through the insect body to reach the salivary glands. Since viruses cannot replicate in an artificial diet, this questions the infectious potential in planta of the viral DNA detected by PCR.

**The Variable Biology of Virus Transmission Demands Replicated Experiments for Proper Interpretation**

Most transmission experiments of GRBV reported in the literature are not replicated (Table I). Replication is essential for verifying findings and promoting the likelihood that the findings were not obtained by pure chance or contamination, thus solidifying the level of confidence in the results. Carrying out a single transmission assay with no replication creates uncertainties and risks the work’s independent reproduction. For example, Bahder et al. (2016) and Kahl et al. (2021) failed to reproduce the findings of Poojari et al. (2013), and Flasco et al. (2021) failed to reproduce the experimental conditions of Bahder et al. (2016) to confirm their findings on S. festinus-mediated transmission of GRBV. Furthermore, understanding the AAP is equally critical for a virus that is transmitted in a circulative mode, as this essential step of the transmission process is highly variable among geminiviruses (Whitfield et al. 2015, Fiallo-Olivé et al. 2021).

By highlighting the unique attributes of GRBV transmission by S. festinus, including a 10-day AAP, we were able to use optimized experimental conditions to confidently identify S. festinus as a vector of GRBV in independent experiments in both the greenhouse (Flasco et al. 2021, Hoyle et al. 2022) and the vineyard (Flasco et al. 2023a).

A range of AAPs, from 48 hrs to 10 days or more, have been used for GRBV transmission assays (Table I). The use of a suboptimal AAP raises doubts about whether the virus has enough time to transit through the insect body and reach the salivary glands following exposure to an infected grapevine. Consequently, a suboptimal AAP does not provide much confidence in transmission results and falls short of documenting the transmission capacity of insect vector candidates. Nonetheless, a variable AAP can be expected, depending on the geminivirus-insect vector pair (Whitfield et al. 2015, Fiallo-Olivé et al. 2020, 2021). Similarly, the inoculation access period (IAP) varied from 48 hrs to several weeks among the different GRBV transmission assays reported so far (Table I), as did the number of insects (one to 25) selected for transmission assays (Table I). Noticeably, fewer S. festinus were necessary to demonstrate transmission of GRBV in the vineyard (Flasco et al. 2023a).

**Detection of Virus in the Salivary Glands is the Gold Standard for Evaluating Insect Vectors of GRBV**

Given the circulative transmission of GRBV (Flasco et al. 2021), an easy approach to determining how meritorious an insect vector candidate is consists of verifying the presence of the virus in the salivary glands, which supports its ability to acquire the virus. Instead of testing whole bodies of insect vector candidates for GRBV by PCR following an AAP on infected grapevines, dissected organs, particularly heads with salivary glands, should be tested. This can be achieved as previously described for S. festinus (Flasco et al. 2021), and illustrated in Figure 2. Testing the presence of GRBV in the salivary glands should be a necessary preliminary step to ascertain the potential of any insect vector candidate to transmit GRBV. If the virus is found in the salivary glands of an insect vector candidate following a gut clearing period so as to avoid confusion related to the presence of GRBV in the gut or mouthparts via ingestion, this species is an excellent candidate for transmission assays. If the virus is not found in the salivary glands of an insect vector candidate given an optimal AAP is applied, this species is unlikely to act as a vector of GRBV.
Excised Leaf Assays Streamline Virus Transmission Experiments

Virus transmission experiments from grapevine to grapevine in the greenhouse are time consuming, resource demanding, and can be technically challenging. Such transmission assays can be simplified by using excised grapevine leaves as virus recipient material instead of potted grapevines (Flasco et al. 2021, Hoyle et al. 2022). Excised leaves are sufficient to document transmission; entire plants are not needed. In addition, the use of excised leaves facilitates the feeding of an insect vector candidate on a restricted plant tissue area, increasing the likelihood of detecting the virus following vector-mediated inoculation (Flasco et al. 2021, 2023a, Hoyle et al. 2022). An additional benefit of excised leaves is that they contribute to the experimental reproducibility of transmission assays. Alternatively, grapevines derived from seedlings could be used as virus recipient plants (Poojari et al. 2013, Kahl et al. 2021). Since GRBV is not seed-transmitted (Flasco et al. 2021), the GRBV-free status of this type of material is ascertained, providing optimal conditions to confidently test the capacity of insect vector candidates to transmit the virus.

Conclusion

Geminiviruses, including GRBV, are usually transmitted in a virus genus-specific manner by distinct arthropod vectors, with transmission being mostly circulative and nonpropagative (Fiallo-Olivé et al. 2021). GRBV is only the second geminivirus for which a treehopper, S. festinus, is documented as a vector. For several decades, tomato pseudo-curly top virus (genus Topocuvirus) was the only geminivirus known to be transmitted by a treehopper, the nightshade treehopper, Micrutalis malleifera (Fowler); however, its transmission mode was not characterized (Simons and Coe 1958). The transmission of GRBV by S. festinus is circulative and nonpropagative (Flasco et al. 2021) with an extended 10-day AAP, in comparison with other geminiviruses (Fiallo-Olivé et al. 2021). Further, S. festinus is a vector of GRBV of epidemiological importance in the vineyard (Flasco et al. 2023a).
In addition to S. festinus, a few other treehopper species have been identified as vector candidates but their capacity to transmit GRBV remains to be solidified (Kahl et al. 2021, LaFond et al. 2022). Additional work will likely generate the data needed to undoubtedly affirm some of these candidates as additional vectors of GRBV. We encourage the scientific community to test the presence of the virus in the salivary glands of insect vector candidates, optimize the AAP, use alfalfa plants for insect gut clearing following virus infection, and include excised grapevine leaves in transmission assays for facilitating the identification of insect vectors of GRBV other than S. festinus. These recommendations should be contemplated as opportunities to address and even alleviate the confusion on how GRBV is transmitted, and by which vector insects. This is critical because reliable information on GRBV transmission from knowledge of virology and vector biology is required to develop strategies for mitigating the impact of red blotch disease in the vineyard and to efficiently communicate scientifically-sound management responses to the grower community.

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ORCID
Madison Flasco 0000-0003-1841-8301
Victoria Hoyle 0000-0003-4106-0168
Elizabeth J. Cieniewicz 0000-0002-2620-4672
Marc Fuchs 0000-0001-5332-6766

Citation

References


