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Potential transmission of grapevine red blotch virus (*Grablovirus vitis, Geminiviridae*) by Nearctic treehopper (*Tortistilus wickhami*) in Baja California, Mexico

Cynthia Ford-Villalón[1], David Schneider[2,3], Idalia Montesinos-Solano[1], Jimena Carrillo-Tripp[1*]. [1]Departamento de Microbiología, [2]Departamento de Biología de la Conservación; Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California, México. Carretera Ensenada-Tijuana No. 3918, Zona Playitas, C. P. 22860. Ensenada, Baja California, México. [3]Facultad de Ciencias, Universidad Autónoma de Baja California. Carretera Tijuana-Ensenada No. 3917. C. P. 22860, Ensenada, Baja California, México.

***Corresponding author:**
Jimena Carrillo-Tripp
jcarrillo@cicese.mx

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ABSTRACT

Background/Objective. Grapevine red blotch virus, GRBV (*Grablovirus vitis*) affects grapevine plants (*Vitis vinifera*) causing significant economic losses in vineyards. In Mexico, where GRBV has been reported in wine-producing regions such as Baja California, information on potential GRBV vectors remains limited. Although the three-cornered alfalfa hopper (*Spissistilus festinus*) is a confirmed vector in the USA, the role of other membracids in vineyards around the globe is still unclear. Recently, the Nearctic treehopper (*Tortistilus wickhami*) has been reported in Baja California, prompting this study to evaluate its potential for GRBV acquisition and transmission.

Experimental development. Adult Nearctic treehoppers were collected from February to November 2023 in 20 vineyards in Valle de Guadalupe, Baja California. A total of 30 individuals were screened to detect GRBV by real-time PCR. In May 2024, 17 additional individuals were collected and used in transmission assays, with an acquisition access period of up to 4 days on GRBV-infected grapevine cv. Cabernet Sauvignon leaves, followed by an inoculation access period of up to 9 days on virus-free leaves. Both insects and recipient leaves were tested for GRBV by real-time PCR.

Results. GRBV was detected in 6.7% (2/30) of the individuals collected in 2023, with positive insects only originating from vineyards confirmed as GRBV-positive. In the transmission assays, 53% (9/17) of the insects acquired viral particles after feeding on infected leaves; however, none of the recipient leaves showed detectable infection.

Conclusion. This study demonstrates that the Nearctic treehopper, an insect phylogenetically close to, and morphologically resemblant of the three-cornered alfalfa treehopper (a confirmed GRBV vector), was able to acquire the virus in the field and in laboratory settings, but no transmission to recipient plants was proved under the tested experimental conditions in the laboratory.

Keywords: GRBV, Transmission, Membracid, Vector

INTRODUCTION

Viticulture is among the most profitable agricultural activities in Mexico (Diaz-Lara *et al.,* 2023a), with Baja California as the leading producer of industrial grape, accounting for 70% of the country's wine production (Moreno-Ortiz, 2025). In 2022, Ensenada was internationally recognized as the second-best destination to enjoy wine, according to the Secretariat of Agriculture and Rural Development (SADER) during the 43rd Congress of the International Organization of Vine and Wine (SADER, 2022).

Grapevine is a perennial crop highly susceptible to a range of pathogens, including numerous viruses (Diaz-Lara *et al.,* 2023b). Among these, grapevine red blotch virus, GRBV (*Grablovirus vitis*) is particularly noteworthy due to its economic impact on the crop. GRBV has a circular single-stranded DNA genome encapsidated in geminate particles (Fiallo-Olivé *et al.,* 2021; ICTV, 2023) and moves systemically through the phloem of infected plants of the genus *Vitis*, which are its only known true hosts (Rumbaugh *et al.,* 2021; Wilson *et al.,* 2022). Infection leads to physiological and metabolic disruptions that reduce yield, delay berry maturation, and alter wine composition and organoleptic qualities (Rumbaugh *et al.,* 2021). Consequently, GRBV imposes a substantial economic burden, with estimated losses reaching USD 68 548/ha over the productive lifespan of a vineyard (Ricketts *et al.,* 2017).

GRBV is primarily transmitted through infected plant material used in grafting and vegetative propagation (Sudarshana *et al.,* 2015). Secondary spread by treehoppers has also been demonstrated, with the three-cornered alfalfa hopper (*Spissistilus festinus*) being the only confirmed vector in the United States (Flasco *et al.,* 2023a). Viral transmission largely depends on specific interactions between the viral capsid protein and insect tissues (Kahl *et al.,* 2021). Consequently, other treehopper species have been suggested as potential vectors, although their role in GRBV epidemiology has not been conclusively demonstrated (Kahl *et al.,* 2021; LaFond *et al.,* 2022).

The Nearctic treehopper (*Tortistilus wickhami*), which belongs to the same tribe (Ceresini) as the three-cornered alfalfa hopper and exhibits behavioral and ecological similarities, suggesting a potential role in virus epidemiology, has also been reported in areas affected by GRBV infections (Hoyle *et al.,* 2024). As part of ongoing efforts to characterize the insect fauna in vineyards of Baja California and its potential involvement in virus dissemination, a previous study documented the occurrence of *T. wickhami* in the region (Schneider *et al.,* 2025), where GRBV has been detected (Gasperin-Bulbarela *et al.,* 2019; García-Reséndiz *et al.,* 2025). The present study evaluated the potential of the Nearctic treehopper (*Tortistilus wickhami*) for GRBV acquisition and transmission, to assess the potential vectoring role of this species. These efforts provide continuity to previous research and offer insight into the epidemiological relevance of this membracid in the vineyards of Baja California.

EXPERIMENTAL DEVELOPMENT

Study site and biological material. Adults of the Nearctic treehopper were collected in 20 vineyards in the Valle de Guadalupe, Baja California, between February and November 2023, as part of a broader survey on vineyard-associated arthropod diversity. Within this context, Schneider *et al*. (2025) were the first to report the presence of the Nearctic treehopper (*T. wickhami*) in the region and described the field sampling scheme applied in the present study. Each site was visited monthly, totaling 10 visits, and plots of 12

grapevines cv. Cabernet Sauvignon were established along vineyard edges, adjacent to natural vegetation, covering an area of approximately 587 m². Specimens were primarily collected using a D-vac aspirator, following the protocol outlined by Schneider *et al*. (2025). From the Membracidae collection of the global project, 30 individuals were selected for this study: eight previously identified by Schneider *et al*. (2025) and 22 newly identified in the present work using morphological analysis and DNA barcoding, following the same methodology. This set constituted the treehopper material used for molecular detection of GRBV. During the described field sampling effort, none of the collected membracids corresponded to the three-cornered alfalfa hopper (*Spissistilus festinus*).

For the transmission assays, 17 live Nearctic treehoppers were manually collected in May 2024. Insects were transported in 950 mL plastic containers with mesh lids, accompanied by fragments of the grapevines on which they were found. Upon arrival at the laboratory, the insects were transferred to pots covered with a mesh containing coyote bush (*Baccharis pilularis*), a native plant not hosting GRBV (Wilson *et al.,* 2022), where they were maintained until the start of the experiment the following day.

To obtain donor material for GRBV transmission, grapevine leaves were collected from vineyards suspected of red blotch disease (based on the presence of characteristic symptoms) at locations where treehoppers were observed during sampling. GRBV-positive leaves (corroborated by real-time PCR) were used as donor material in the transmission assays. GRBV-free vines cv. Cabernet Sauvignon obtained from Guillaume Grapevine Nursery Inc. (Paso Robles, California, USA) confirmed as negative by real-time PCR, served as the recipient material. Insects and leaves collected in the field for molecular analyses were transported to the laboratory in coolers with ice packs. Upon arrival, insects were transferred to 1.5 mL microcentrifuge tubes containing 95% ethanol, and both insects and leaves were stored at –20 °C until further processing.

Real-time PCR (qPCR) detection of GRBV. Prior to detection, insects were washed twice with 70% ethanol, followed by a rinse with molecular-grade water under gentle vortexing to remove any viral particles adhering to their surface. Total DNA was extracted from both membracids and grapevine tissue using the CTAB method described by Lodhi *et al.* (1994). GRBV detection was conducted via qPCR using two primer pairs described by Krenz *et al*. (2014), the CPfor/CPrev pair targets the coat protein gene (*cp*), while Repfor/Reprev amplifies a region of the replication-associated protein gene (*rep*). rt-PCR reactions were carried out in a final volume of 10 µL containing 0.1 µL of DreamTaq DNA Polymerase (Thermo Scientific™) and EvaGreen® Dye (20× in water, Biotium Glowing Products of Science™), 1 µL of 10× DreamTaq buffer (Thermo Scientific™), 0.2 µL of dNTP mix (10 mM each), 500 nM of each primer, and 1 µL of DNA template (150 ng μL^{-1}). Thermal cycling conditions were as follows: initial denaturation at 95 °C for 3 min, followed by 40 cycles of 94 °C for 15 s, 61 °C for 30 s, and 72 °C for 15 s. A melting curve was performed from 65 °C to 95 °C, with 0.5 °C increments every 0.05 s. Reactions were run in a CFX96™ C1000 Touch™ Real-Time PCR Detection System (Bio-Rad™ Laboratories, Hercules, CA, USA), and data analysis was performed using CFX Manager™ software version 3.0 (Bio-Rad™ Laboratories). Each sample was analyzed in duplicate. Samples were considered positive for GRBV only if amplification occurred with both primer sets and met all of the following criteria: a Cq value below 30 cycles, a fluorescence signal above the threshold [60 relative fluorescence units (RFU)], melting temperatures (Tm) within the reference range for GRBV-positive samples (84.0 ± 1 °C). All real-time PCR assays were performed alongside a non-template control (NTC) and two

positive controls: (1) a plasmid containing a 1.9 Kb fragment of GRBV encompassing partial *cp* and *rep* gene regions (Palacios, 2019), and (2) genomic DNA from GRBV-infected plants collected at a confirmed vineyard site. For plant tissue, an internal control was included targeting the *rbcL* gene using the Rbc1-F/Rbc1-R primer pair (Sánchez-Navarro *et al.,* 2005), under the same cycling conditions as GRBV detection. For membracids, a fragment of the 18S rRNA gene was amplified using primers Sf18SFor/Sf18Srev (Flasco *et al.,* 2023a).

Insect taxonomic identification. All the specimens used in this study were identified using a morphological approach, complemented with molecular identification in some cases, as previously reported (Schneider *et al*., 2025). Morphological identification included examination of the male genitalia and species determination using reference taxonomic keys (Caldwell, 1949; Dietrich and Dmitriev, 2006). Molecular identification was based on sequencing the *co1* barcode gene. PCR amplicons were purified and sequenced by Macrogen Inc. (Gyeonggi-do, South Korea), and sequence editing, alignment, and consensus generation were performed using BioEdit (Hall, 1999). Species identity was verified through similarity searches using BLAST (Altschul *et al*., 1990) and the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert, 2007). All the new sequences were deposited in the GenBank database; accession numbers are provided in Tables 1 and 2.

Field survey. Individual results for all the membracids from the field survey, including molecular assay data, are provided in Table 1. Among the visited sites, four vineyards were suspected of red blotch infection based on the presence of red leaves on some plants, but only two vineyards were confirmed positive for GRBV. In these last, GRBV was detected in two Neartic treehopper individuals (6.7%, 2/30), suggesting a potential association between this insect and the virus; although detection alone does not imply vector competence. This prevalence is consistent with the findings of Hoyle *et al.* (2024), who reported GRBV in 6% (48/758) of individuals of the same species, as compared to 23% (59/259) in the three-cornered alfalfa treehopper (*S. festinus*). The positive individuals in our study were collected during June and July, a period that aligns with previous detections of GRBV in vectors starting in June (Hebert *et al.*, 2003; Cieniewicz *et al.*, 2018), indicating that viral acquisition may begin early in the summer, when the reduction of alternative hosts increases feeding on grapevines and, consequently, the likelihood of virus transmission (Preto *et al.*, 2019).

GRBV transmission assay. To assess the virus transmission capacity, Nearctic treehoppers were allowed to feed on GRBV-infected grapevine cv. Cabernet Sauvignon leaves for an acquisition access period (AAP) of up to four days. Surviving insects were subsequently transferred to cages containing GRBV-free grapevine cv. Cabernet Sauvignon leaves and maintained for up to nine days of inoculation access period (IAP), with systematic monitoring of mortality (Figures 1 and 2). The experiment was conducted in the laboratory at room temperature, with daily temperatures of 18–22 °C (maximum) and 11–15 °C (minimum), under a natural photoperiod (14 h/10 h light/dark). Individuals that died during the assay were progressively removed from the cages and immediately preserved in 95% ethanol, while recipient leaves were maintained in tubes with water throughout the experimental period to maximize the potential for viral replication; all biological materials were then stored at –20 °C until GRBV detection by real-time PCR as described above.

Table 1. Taxonomic identification of treehoppers collected at survey sites, and GRBV molecular detection.

Num.	Collection month (2023)	Vineyard (site)	Identification		GRBV detection (qPCR)	GenBank accession number [x]
			Morphology	Molecular [x]		
1	May	1	*T. wickhami*	*T. wickhami*	-	PX136203 [z]
2	May	1	*T. wickhami*	*T. wickhami*	-	PX136206 [z]
3	May	1	*T. wickhami*	*T. wickhami*	-	PX136207 [z]
4	May	1	*T. wickhami*	na	-	na [z]
5	May	1	*T. wickhami*	na	-	na [z]
6	May	2	*T. wickhami*	*T. wickhami*	-	PQ509407 [y]
7	May	2	*T. wickhami*	*T. wickhami*	-	PQ513532 [y]
8	May	2	*T. wickhami*	*T. wickhami*	-	PX136202 [z]
9	May	2	*T. wickhami*	*T. wickhami*	-	PQ514004 [y]
10	May	2	*T. wickhami*	*T. wickhami*	-	PX136205 [z]
11	May	3	*T. wickhami*	na	-	na [z]
12	May	4	*T. wickhami*	na	-	na [z]
13	May	4	*T. wickhami*	*T. wickhami*	-	PQ516711 [y]
14	June	1	*T. wickhami*	na	-	na [z]
15	June	1	*T. wickhami*	na	-	na [z]
16	June	1	*T. wickhami*	na	-	na [z]
17	June	1	*T. wickhami*	na	-	na [z]
18	June	2	*T. wickhami*	*T. wickhami*	+	PQ520535 [y]
19	June	2	*T. wickhami*	na	-	na [z]
20	June	3	*T. wickhami*	na	-	na [z]
21	June	3	*T. wickhami*	na	-	na [z]
22	June	5	*T. wickhami*	na	-	na [z]
23	June	5	*T. wickhami*	*T. wickhami*	-	PQ516700 [y]
24	June	5	*T. wickhami*	*T. wickhami*	-	PX136204 [z]
25	June	5	*T. wickhami*	na	-	na [z]
26	July	4	*T. wickhami*	na	-	na [z]
27	July	5	*T. wickhami*	*T. wickhami*	-	PX136201 [z]
28	July	5	*T. wickhami*	*T. wickhami*	+	PQ516698 [y]
29	July	5	*T. wickhami*	*T. wickhami*	-	PQ520534 [y]
30	July	5	*T. wickhami*	na	-	na [z]

[x] na, not applicable, the individual's DNA was not tested, identification was based on morphology.

[y] Individuals previously identified by Schneider *et al.* (2025).

[z] Individuals newly identified in the present study.

Individual results for all insects of the assay, are provided in Table 2. Of the 17 initial individuals, 53% (9/17) died before completing the four-day AAP, while the remaining 47% (8/17) proceeded to the inoculation phase. Among these survivors, 75% (6/8) died during the IAP, and only 25% (2/8) completed the planned four-day IAP, remaining an additional five days on the recipient leaves. In comparison to the mortality of our AAP, the three-cornered alfalfa hopper exhibits mortality rates of 10–20% within 48 hours after exposure to infected grapevines, requiring 30–40 individuals to transfer six to eight survivors to the IAP (Flasco *et al*., 2021). In this study, GRBV was detected in 53% (9/17) of the individuals, irrespective of exposure time to donor leaves. Since the insects used in our transmission assay were collected from a vineyard with GRBV presence, the possibility of prior viral load cannot be ruled out. However, when comparing the ingestion rate observed in the assay with the prevalence of GRBV in insects collected from the same vineyard (14% (1/7)), the results highlight the efficiency of active viral acquisition under controlled conditions and exclusive exposure to infected material. In comparison, Bahder *et al*. (2016) reported 75% (15/20) acquisition in the three-cornered alfalfa hopper after 48 hours of exposure to infected grapevines. Similarly, *T. albidosparsus* carried the virus in 60% (3/5) of cases in a greenhouse setting and 25% (1/4) in the laboratory, both with an AAP of six days (Dalton, 2020).

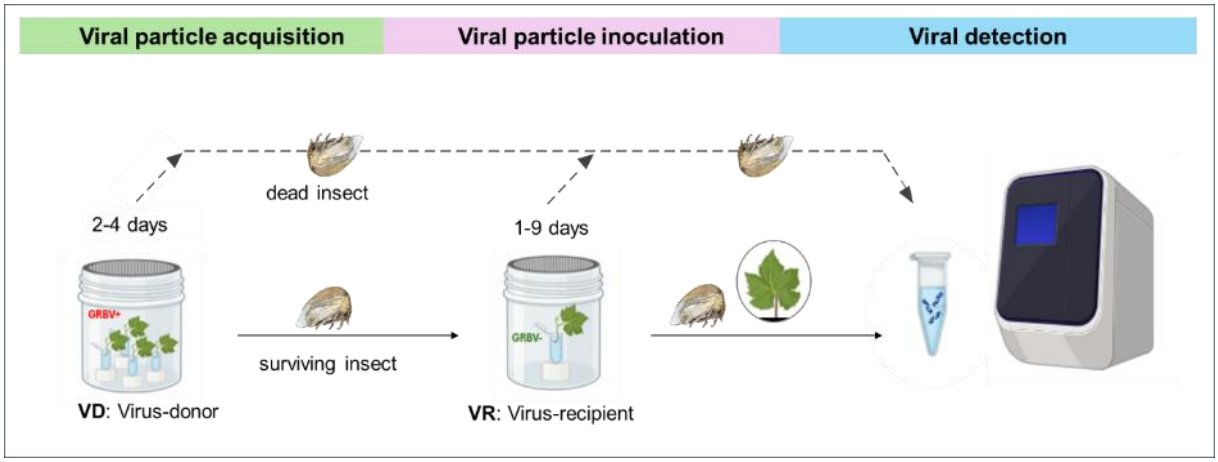

Figure 1. Schematic representation of the GRBV transmission assay. Insects were first allowed to feed on excised leaves from a GRBV-donor grapevine, then transferred to recipient excised leaves from GRBV-free grapevines to assess potential virus transmission. Individual leaves were maintained in water. Dashed lines indicate the removal of dead insects from inside the cage for GRBV detection at the end of the assay. The schematic diagram was constructed using some elements from BioRender.

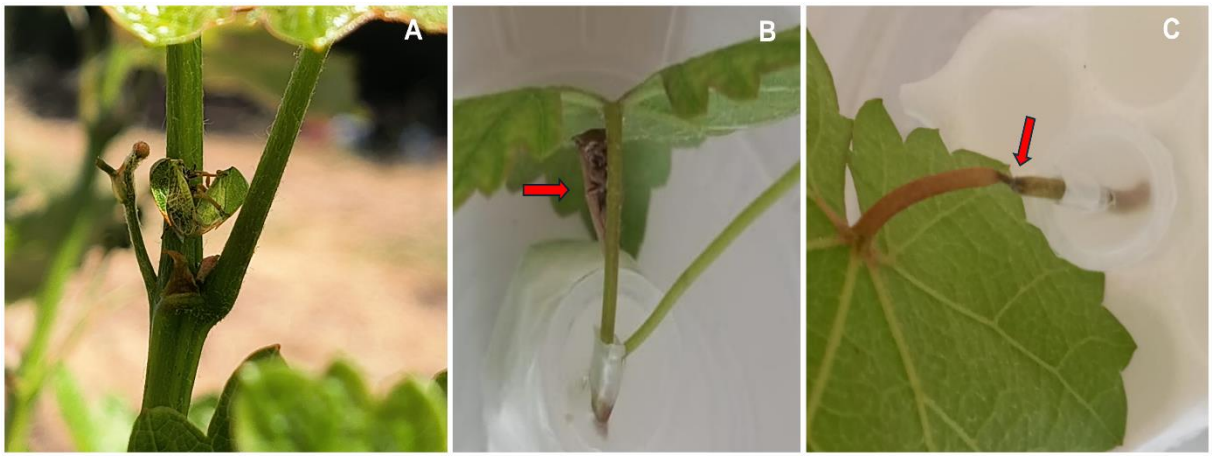

Figure 2. Transmission assay. **A**) Example of adult Nearctic treehoppers manually collected from a vineyard, used in the transmission assay. Photo credit: Kyara Acosta Ramos. **B**) interior view of a cage during the viral particle acquisition phase. The cage design facilitated insect–leaf interaction. A portion of the petioles were submerged in sterile water inside 2 mL vials sealed with parafilm, keeping the leaf in a vertical position. **C**) Ringing mark on the petiole of a recipient leaf caused by mechanical damage after feeding by a Nearctic treehopper.

Successful feeding was evidenced by a ring-shaped mark on the petiole of a recipient grapevine leaf (Figure 2C); however, no viral titers were detected. The lack of transmission could be due to insufficient periods of inoculation and acquisition access, likely limiting the virus from reaching the salivary glands, the key organ for transmission (Flasco *et al*., 2023b). Flasco *et al.* (2021) reported that GRBV is detectable in the gut of the three-cornered alfalfa hopper after five days and in the head and salivary glands after ten days. Hoyle *et al*. (2024) did not detect the virus in any of the 50 *T. wickhami* heads analyzed; nevertheless, GRBV prevalence in the surveyed vineyards ranged from 1 to 78%, and it is unknown whether the dissected insects came from areas of high or low incidence. Since the insects fed freely on both healthy and infected plants, it is impossible to determine whether the AAP was sufficient for the virus to reach the key organ for transmission. By contrast, in *T. albidosparsus*, GRBV has been detected in the abdomen and salivary glands

of 1 out of 20 individuals (Zalom *et al*., 2019), indicating that acquisition can occur under specific conditions. Further research investigating the tissue tropism of GRBV in the Nearctic treehopper would provide valuable insights.

Table 2. Results of the transmission assay for GRBV (*Grablovirus vitis*) by adult Nearctic leafhoppers.

Num.	AAP[x]	IAP[y]	Identification		GRBV detection (qPCR)		Gen Bank accession number[z]
			Morphology	Molecular[z]	Insect	Recipient leaves	
1	4 d	9 d	*T. wickhami*	na	–	–	na
2	4 d	9 d	*T. wickhami*	na	–	–	na
3	4 d	< 1 d	*T. wickhami*	*T. wickhami*	+	–	PV684988
4	4 d	< 1 d	*T. wickhami*	*T. wickhami*	+	–	PV684989
5	4 d	< 1 d	*T. wickhami*	na	–	–	na
6	4 d	< 1 d	*T. wickhami*	na	–	–	na
7	4 d	< 1 d	*T. wickhami*	*T. wickhami*	+	–	PV684990
8	4 d	< 1 d	*T. wickhami*	na	–	–	na
9	< 4 d	……	*T. wickhami*	*T. wickhami*	+	–	PV684991
10	< 4 d	……	*T. wickhami*	*T. wickhami*	+	–	PV684992
11	< 4 d	……	*T. wickhami*	*T. wickhami*	+	–	PV684993
12	< 4 d	……	*T. wickhami*	na	–	–	na
13	< 4 d	……	*T. wickhami*	na	–	–	na
14	< 4 d	……	*T. wickhami*	*T. wickhami*	+	–	PV684994
15	< 4 d	……	*T. wickhami*	*T. wickhami*	+	–	PV684995
16	< 4 d	……	*T. wickhami*	*T. wickhami*	+	–	PV684996
17	< 4 d	……	*T. wickhami*	na	–	–	na

[x] AAP, acquisition access period in days (d). [y]IAP, inoculation access period in days (d); ……, insect died before the IAP. [z]na, not applicable, the individual's DNA was not tested; identification was based on morphology. All the insects were identified in the present study.

CONCLUSIONS

The detection of GRBV by rt-PCR in the Nearctic treehopper (*Tortistilus wickhami*) individuals collected in the field, alongside the preliminary transmission assays results, indicate that this species can acquire viral particles during feeding in natural and controlled conditions. However, no propagation of GRBV was observed in the transmission assays conducted in this study.

Together with the findings reported by Hoyle *et al*. (2024), these results indicate that the Nearctic treehopper does not act as a vector of GRBV. Therefore, despite its presence in vineyards where the virus has been detected, the available evidence suggests that this species does not contribute to the transmission or epidemiology of GRBV in vineyards. A result relevant for field technicians in charge of developing vineyard management plans.

Limitations. An important challenge for virus transmission experiments involving membracids is the establishment of laboratory colonies. Zalom *et al*. (2018) reported that reproductive colonies of *Tortistilus* could not be successfully maintained, highlighting the fragility of these insects outside their natural habitat. Accordingly, the transmission protocol in this study was adjusted based on insect survivorship observed in preliminary trials (data not shown). To address these constraints, transmission assays were conducted

using excised grapevine leaves rather than whole plants, which may represent a limitation because GRBV is a phloem-limited virus. However, excised leaves have also been used as recipient material in GRBV transmission experiments. In the study by Flasco *et al.* (2021), detached leaves were used exclusively as recipient tissue, whereas virus acquisition occurred on whole grapevines.

Disclosure statement. The authors declare they do not have any conflicts of interest.

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Authors' contribution. Conceptualization: JC-T, DS; Methodology: CF-V, DS, IM-S; Sampling and data analysis: CF-V, DS; Funding acquisition: JC-T; Supervision: JC-T, DS, IM-S; Writing-original draft: CF-V; Writing-review and editing: CF-V, IM-S, DS, JC-T.

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