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Grapevine Red Blotch Disease: A Threat to the Grape and Wine Industries

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Abstract

Grapevine red blotch disease emerged as a major threat to the North American viticulture more than 25 years ago. Prior to the discovery of its causal agent, grapevine red blotch virus (GRBV), the disease was likely mistaken for other vineyard problems. Over the last decade and a half, research on red blotch disease focused on GRBV biology; diagnostics; transmission biology; disease epidemiology; ecology of its vector, the treehopper *Spissistilus festinus*; and strategies for disease management. Research has also uncovered some of the physiological effects of GRBV on grapevines (inhibition of hexose translocation from leaves to fruits, transcriptional suppression of phenylpropanoid pathways), fruit (low soluble solids, poor ripening, reduced phenolic extractability, high titratable acidity), and wine (altered sensory attributes such as less fruit aromas and poor color and mouthfeel). The economic effects of the disease in different grape-producing regions of the United States are estimated to be as high as \$68,548 per hectare over a 25-year vineyard lifespan. Here we reflect on major red blotch research progress and discuss future priorities. We also highlight the contribution of GRBV to the grapevine community as a major driver of enhanced cooperation among researchers, growers, nurseries, extension agents, policymakers, regulators, and service providers. We anticipate that strengthened interactions among all the members of the grapevine community and science-based disease management responses in vineyards will curtail GRBV spread and improve vineyard health.

4.1



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INTRODUCTION

Viruses affect nearly every crop globally, in some cases causing significant losses in yield and quality (1). In addition to the direct effects that disease-causing viruses have on crop plants, viruses are a critical and understudied component of the phytobiome (2). Grapevine (*Vitis* spp.) is host to 102 viruses, although only a fraction of these viruses have noticeable effects on grapevine health or fruit quality (3, 4). In a little over a decade, there has been more than a 540% increase in the number of virus species ratified by the International Committee on the Taxonomy of Viruses (5). The availability of advanced genomics technologies over the last two decades has resulted in a boom in virus discovery and a shifting paradigm in virology. Prior to the availability of high-throughput sequencing, virus discovery was typically prompted by an aberrant phenotype and some biological characterization such as effect on plant health and production, host range, and virion properties. Now, numerous viruses are being discovered often without any relation to known disease etiologies. Research on grapevine red blotch virus (GRBV) has been at the intersection of this shifting paradigm in plant virology. Here we review the current knowledge on GRBV in terms of its biology, ecology, epidemiology, transmission, and management (Figure 1) and offer perspectives on promising directions for GRBV research.

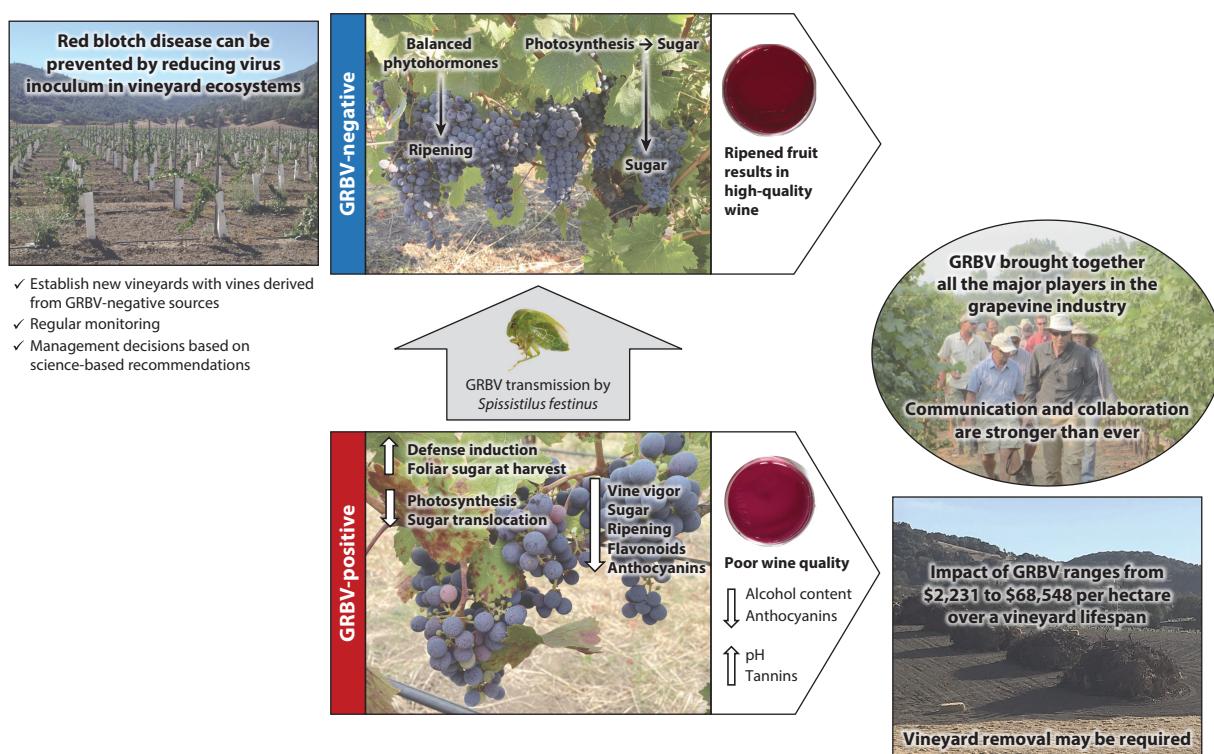


Figure 1

Overview of the physiological, economic, and social effects of grapevine red blotch virus (GRBV), transmission of GRBV by *Spissistilus festinus*, and disease management strategies. We emphasize the importance of establishing new vineyards using vines derived from GRBV-negative stocks and implementing science-based disease management. The emergence of red blotch disease has necessitated strategic communication among the major players in the grapevine industry, resulting in strong interaction and collaboration among the industry members, regulatory bodies, researchers, and extension educators.



DISCOVERY AND DISTRIBUTION

Grape growers in California noticed poor fruit quality in several vineyards starting in the early to mid-2000s. At harvest, fruits of red-berried wine grape cultivars often had pale berry skin color, and fruit juice had substantially lower sugar levels. Also, leaves of red-berried grape cultivars became atypically red prior to harvest, and the reddening persisted through the remainder of the growing season. Based on these observations, the occurrence of leafroll disease, which causes similar anomalies, was suspected in the symptomatic vines, or, alternatively, the existence of a new disease was alleged (6). The same conditions as those identified by growers in commercial vineyards were recognized in 2008 at an experimental vineyard managed by the University of California, Davis (7). However, viruses associated with leafroll disease were not detected in vines exhibiting these unusual symptoms. Therefore, the condition of poorly performing vines was plausibly explained by a new disease, which was referred to as red blotch. This disease name—red blotch—was inspired by the type of coloration observed on leaves of affected red-berried vine cultivars.

In March 2011, Keith Perry and his colleagues at Cornell University serendipitously detected a viral DNA molecule in poorly performing vines in an experimental New York vineyard by rolling circle amplification in combination with restriction fragment length polymorphism and sequencing (8). The monopartite single-stranded, circular DNA genome of this novel virus codes bidirectionally for seven open reading frames (ORFs) (9, 10) and is 3,206 bp in size with similarities to geminiviruses (8). However, the genome is larger and has limited sequence identity, particularly with begomoviruses in the viral sense ORF coding the coat protein, and predicted spliced transcripts, like for mastreviruses, for two complementary-sense ORFs. In an independent study, Maher Al Rwahnih and his colleagues at the University of California, Davis identified the same viral genome in the summer of 2011 by high-throughput sequencing in an effort to characterize viruses in vines exhibiting red blotch disease symptoms (11). The UC-Davis group referred to this virus as grapevine red blotch-associated virus. Extensive surveys of diseased vineyards in California in 2012 and 2013 documented a high association (97%) between symptomatic vines and the occurrence of the virus (11). The same virus was later described in Washington State (12) and Oregon (13). By fulfilling Koch's postulates with infectious virus clones, grapevine red blotch-associated virus was shown to cause red blotch disease, justifying its current name, grapevine red blotch virus (GRBV) (14).

In a decade and a half of GRBV research, virions have yet to be visualized. Although mass spectrometry detected protein products of the GRBV V1 (coat protein) and V2 (movement protein and silencing suppressor) ORFs (15), detection and visualization of GRBV particles still eludes researchers. A lack of comprehensive understanding of the expression of viral proteins hampers our abilities to purify immunogenic virions and/or develop serological assays for GRBV detection. DNA testing by DNA amplification techniques is the only reliable diagnostic method for GRBV (11, 16–19). Several PCR assays, including simplex or multiplex end-point assays and real-time assays, were developed for routine diagnostics purposes. Petioles of fully expanded leaves collected in late summer and fall are recommended for an accurate diagnosis (11, 19). More recently, an AmplifyRP® Acceler8® (18), a plasmonic CRISPR Cas12a assay (20), and a loop-mediated isothermal amplification (LAMP) assay (21) were developed. Some growers in Napa Valley, California, are using LAMP for large-scale, on-site testing (22). In addition, hyperspectral imaging spectrometry has been explored as a remote sensing technology (23). Different types of detection and diagnostic assays will help to address different research gaps, and efforts should continue to be focused on developing and refining these assays.

Following the development of reliable laboratory diagnostic tools, GRBV was quickly found in vineyards throughout the United States (16) and Canada (24–26). The virus was also documented



in South Korea (27), Mexico (28), Argentina (29), India (30), and Iran (31). Such a wide geographic distribution of GRBV is explained by the exchange of infected propagative material and/or planting stocks. The presence of GRBV was also described in germplasm repositories in Switzerland (32), Italy (33), France (34), and Australia (35). The occurrence of the virus in germplasm collections is likely explained by the introduction of infected material from California prior to the discovery of the virus. Bayesian analyses on heterochronous data including 163 complete genome sequences of GRBV suggest that GRBV divergence from the ancestral wild *Vitis* latent virus occurred around 9,000 years ago (36). Notably, this proposed speciation event, long before the arrival of *Vitis vinifera*, the European wine grape, in North America, suggests a North American origin for GRBV (36).

GRAPEVINE RED BLOTCH VIRUS BIOLOGY

The GRBV genome is a single molecule of circular, single-stranded DNA with seven putative ORFs, three in the complementary orientation and four in the viral orientation. Initially, six functional ORFs were predicted (8), but later an additional ORF in the viral sense, named ORF0, was identified by RNA sequencing, although the function of V0 is still unknown (10). Although some ORFs have no ascribed function, the Rep-associated protein, critical to genome replication, is a result of a splicing event fusing the C1 and C2 ORFs, consistent with other geminiviruses. A role in movement has been proposed for the V2 and V3 ORFs based on subcellular localization (37), and V1 is the predicted coat protein. ORFs C2 and V2 have silencing suppressor activity, though the mechanisms of suppression of transcriptional and/or post-transcriptional gene silencing are unknown (38).

There are two major phylogenetic lineages of GRBV sequences with several recombinant variants in wine grape cultivars and free-living *Vitis* species (16, 36, 39–42). Representative sequences from both phylogenetic clades were used for generating infectious virus clones and fulfilling Koch's postulates with both clones eliciting red blotch disease symptoms (14). To date, no biologically significant differences between GRBV lineages have been shown and there is no link between GRBV genotype and symptom expression.

EFFECT ON WINE GRAPES

GRBV substantially affects grape yield, berry quality, and wine composition and sensory attributes, particularly in red wine grape cultivars such as Cabernet franc, Pinot noir, Cabernet Sauvignon, Syrah, and Merlot. Foliar symptoms typically appear after véraison, the onset of fruit ripening, as red/purple blotches on the older leaves of red wine cultivars, whereas the irregular chlorosis symptoms are less obvious in white wine cultivars. GRBV reduces photosynthesis and transpiration (32), disrupts grape berry ripening pathways, and activates metabolic pathways associated with early berry development, which results in reduced flavonoid and anthocyanin accumulation. Effects of GRBV on wine grapes also include disruption of hormonal pathways such as abscisic acid, ethylene, and auxin, which affect berry ripening (43), as well as alteration of cell wall composition of grapes, resulting in decreased phenolic extraction in the winemaking process (44). GRBV is associated with reduced fruit sugar content at harvest (32, 45) but higher foliar sugar levels, indicating disruptions in carbohydrate translocation that cannot be adequately remedied by source-sink manipulation (**Figure 1**) (46). GRBV induction of plant defenses is also associated with reduced fruit quality (43, 47). Chaptalization, i.e., the addition of sugar to fruit juice prior to fermentation, and delayed harvest may improve wine quality from GRBV-infected fruit (48, 49), and supplemental irrigation may improve vine physiology and fruit quality (50). However, results of these mitigation responses are inconsistent with variations observed across vineyard sites



and from year to year. In addition, although these mitigation practices are of potential immediate interest to improve wine quality, they do not address disease management by reducing the virus inoculum and preventing spread of the virus.

The effects of GRBV on fruit and wine quality are estimated to range from \$2,231 to \$68,548 per hectare over the supposed 25-year vineyard lifespan (51). The economic effects are dependent on the viticulture region, cultivar, virus incidence, and costs of disease control and vineyard management, as documented in California's Napa and Sonoma Counties, eastern Washington, and Long Island, New York, where price penalties for lower-quality fruit vary (51). Based on their economic analysis, Ricketts et al. (51) recommended a strategy to use a 30% disease incidence cutoff in deciding whether to remove the full vineyard (>30%) or rogue and replace individual vines with clean vines (<30%), which has held up as a solid disease management recommendation in practice.

EPIDEMIOLOGY AND ECOLOGY

The identification of factors driving the spread of GRBV has been a research priority since the virus was discovered. This priority has merit because knowledge of virus ecology can translate almost immediately into optimal strategies for disease management. Significant efforts by multiple research groups have enhanced our understanding of GRBV spread. Because GRBV is efficiently transmitted through vegetative propagation (i.e., cuttings and grafting) (16), it quickly became clear that GRBV should be added to the testing regime for clean plant programs and certification programs in the United States and Canada. Considering the likelihood that GRBV had been disseminated predominantly through planting material prior to its discovery in 2011, the next logical questions to address were related to secondary spread in vineyard ecosystems, which spurred a race to identify a vector and prompted efforts to identify inoculum sources in and around vineyards.

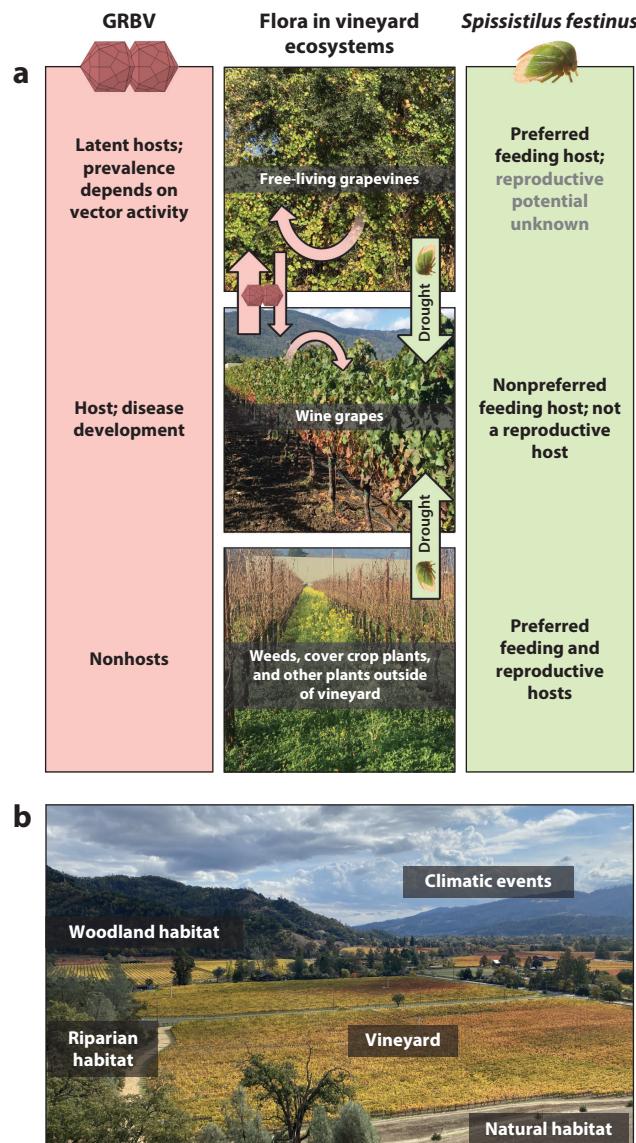
Based on initial observations of secondary spread of GRBV in California, identification of the vector became an urgent priority. Bahder et al. (52) suggested *Spissistilus festinus*, the three-cornered alfalfa hopper, as a vector of GRBV in greenhouse transmission studies. Concurrently, multiyear studies in a vineyard in Napa Valley, California, documented secondary spread of GRBV (53) and identified *S. festinus* as a candidate vector (54), suggesting its potential relevance as a vector in vineyards. These studies formed the foundation for the next decade of research on GRBV ecology.

Vitis species are the only known natural host of GRBV. The virus is reported in wine grapes (6, 11, 53), table grapes (55), interspecific hybrids (41, 56), muscadines (57), and rootstocks (6, 9, 11). It also occurs in free-living vines in northern California (17, 39, 40, 58) and southern Oregon (59), but not in New York (60). Snap bean (*Phaseolus vulgaris*) is a pseudosystemic host of GRBV in the laboratory, and alfalfa (*Medicago sativa*) is a nonhost (61, 62). Surveys of weeds and cover crops in vineyard ecosystems have found no additional hosts of GRBV (58, 60).

Although GRBV has been detected in free-living vines, their significance as virus inoculum sources for secondary spread is unclear (40). Although *S. festinus* can transmit GRBV between free-living vines and *V. vinifera* in the laboratory (62), a connectivity between the three-cornered alfalfa hopper and free-living vines in riparian areas proximal to vineyards in northern California was only recently documented, highlighting their involvement in red blotch disease epidemiology (Figure 2) (63).

Infected planting material is often the primary GRBV inoculum source in the vineyard, but dynamics of secondary spread are regionally nuanced. Overall, annual increases in disease incidence of 0.3–28% have been reported in vineyards (53, 59, 60, 64, 65). In Napa Valley, California,



**Figure 2**

(a) Summary of ecological knowledge on grapevine red blotch virus (GRBV), including plant hosts of both the virus and the vector, *Spissistilus festinus*. Pink arrows indicate the direction of virus spread, with relative arrow sizes indicating efficiency, and green arrows indicate how weather conditions drive *S. festinus* dispersal behavior in vineyard ecosystems. (b) View of a vineyard ecosystem illustrating habitats and factors that contribute to GRBV spread.

one vineyard site planted with Cabernet franc in 2008, surrounded by a riparian habitat and other vineyard parcels with red wine cultivars, has provided a unique opportunity to understand secondary spread of GRBV over a decade (39, 53, 54, 60, 65, 66). The ability to study long-term virus spread dynamics in vineyards is rare because oftentimes the crop is uprooted when virus spread is confirmed and/or the effects of the disease cause a reduction in profitability. It is important to



mention that the series of studies that used the Cabernet franc site in Napa Valley over more than 10 years was possible due to concerted communication between researchers, the owners of the estate, and the vineyard management personnel, as well as a mutual trust.

The Cabernet franc vineyard was planted in 2008, and aspects of GRBV spatiotemporal spread were studied from 2014 to 2023, revealing that secondary spread was primarily within-vineyard (53) and spatially associated with *S. festinus* populations (54). The dispersal of *S. festinus* within the vineyard related to varying levels of virus incidence and aggregation. In vineyard areas with high disease incidence and aggregated spatial patterns, a logistic model provided the best fit of spread, while in areas with lower disease incidence and aggregated spatial patterns, an exponential model provided the best fit of spread and spatiotemporal spread was random (67). Furthermore, precipitation and temperature significantly influenced epidemic parameters three years later. Indeed, disease incidence measured by visual inspection of vines for typical disease symptoms increased three years after an extended drought period with high seasonal temperatures (**Figure 2**) (67). This statistically supported association between weather events and disease incidence suggested a long (i.e., three year) disease incubation period. It would be interesting to experimentally validate this observation. Additionally, an inverse spatial prevalence of GRBV strains 1 and 2 in the Cabernet franc vineyard suggested secondary spread mostly from diseased to neighboring vines combined with virus influx from background sources. Finally, asymptomatic infections, particularly in vineyard areas with lower disease incidence, contributed to spatial aggregations of infected vines at increasing distances from symptomatic vines (67). In vineyard sites neighboring the Cabernet franc vineyard, distinct aggregation levels and spread patterns were observed (60, 65). Patterns of GRBV aggregation were also observed in Oregon vineyards (59, 64). The rate of disease spread appears to be dependent on the initial GRBV incidence in vineyards, the abundance of *S. festinus*, and weather events (53, 60, 65, 67). Recent work indicated a high incidence of asymptomatic infections in some areas of diseased vineyards, suggesting that such inoculum that is hidden to the naked eye likely substantially contributes to secondary spread (67, 68). Secondary spread of red blotch disease was not documented in a New York vineyard (60) nor in germplasm repositories in Switzerland (32), Italy (33), and France (34). Similarly, in a 28-year-old vineyard in Dahlonega, Georgia, in which both GRBV and *S. festinus* are present and the GRBV incidence is approximately 8%, there has been no evidence of GRBV spread over three years (E. Cieniewicz, unpublished data). The results obtained in Europe might be explained by the absence of *S. festinus* in these regions, whereas the lack of observed secondary spread of GRBV in Georgia may be explained by the year-round abundance of preferred feeding hosts of *S. festinus* outside vineyard settings.

S. festinus is a well-known pest of leguminous crops such as alfalfa, soybeans, and peanuts in the United States (69, 70). In contrast, this treehopper is not a direct pest of grapevines, although it can girdle shoots and petioles while feeding (62, 66, 71, 72). *S. festinus* uses wine grapes as an opportunistic host; it does not reside in vineyards and does not survive on these plants past their third molt (71). Vector populations are typically found in northern California vineyards from March to November with peak visibility during the early summer months (May to June) and a substantial tapering off toward the end of July (54, 72, 73). Interestingly, *S. festinus* uses a wide range of diverse plants of the families *Asteraceae*, *Fabaceae*, *Vitaceae*, *Plantaginaceae*, *Poaceae*, *Fagaceae*, and *Solanaceae* as feeding hosts in vineyard ecosystems (63). Among *Vitaceae*, free-living vines are predominantly visited by *S. festinus*, but their role as reproductive hosts of this treehopper is not known yet (**Figure 2**). The role of free-living vines in GRBV ecology should be addressed to better understand red blotch disease epidemiological attributes in the early phases of an epidemic.



GRAPEVINE RED BLOTH VIRUS TRANSMISSION BY *SPISSISTILUS FESTINUS*

GRBV is a geminivirus (species *Grablovirus vitis*, genus *Grablovirus*, family *Geminiviridae*). Geminiviruses are phloem limited and categorized into 14 distinct genera based on their phylogenetic relationships, genome organization, host range, and insect vectors (74, 75). Transmission is achieved in a virus-genus-specific manner by distinct arthropod vectors, including whiteflies (begomoviruses), aphids (capulaviruses), treehoppers (grabloviruses, topocuviruses), and leafhoppers (becurtoviruses, curtoviruses, mastreviruses, mulcileviruses, turncurtoviruses) (74). Insect vectors of citlodaviruses, eragroviruses, maldoviruses, opunviruses, and topileviruses are unknown (74, 75).

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 (74, 76). Transmission starts with the insect feeding on the phloem sap of infected plants. 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 3**). A prerequisite for geminivirus transmission is that virions must be acquired in the salivary glands (76–79). After acquisition, the virus is transmitted upon feeding into the phloem of host plants via the salivary canal. 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 (78, 79). Given a circulative transmission, testing the whole bodies of vector candidates informs their capacity to ingest the virus but not to transmit it; it is only the testing of dissected salivary glands that indicates whether a vector candidate is potentially capable of transmitting GRBV (80). For example, GRBV was detected in whole bodies of *Tortistilus wickhami* caught in diseased vineyards by PCR but not in the salivary glands, making this treehopper species an unlikely vector (81).

The identification of arthropod vectors of GRBV has created substantial confusion. Several species of *Cicadellidae* and *Membracidae*, including *S. festinus*, have been reported to transmit GRBV

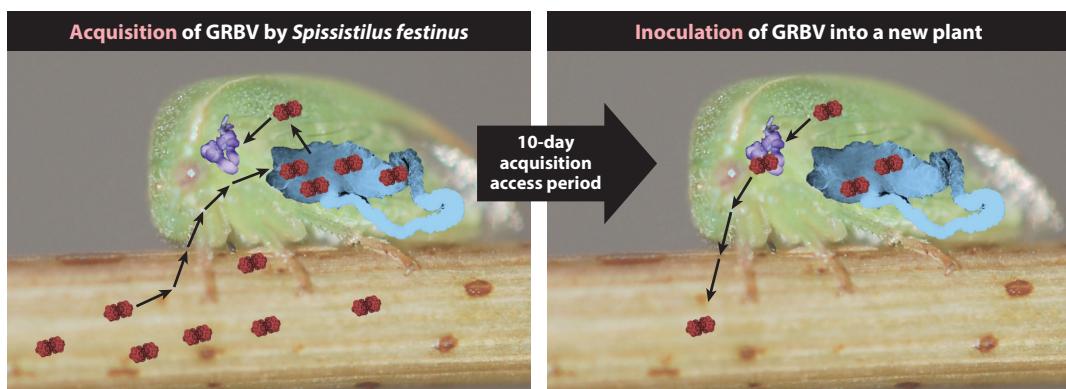


Figure 3

Grapevine red blotch virus (GRBV, depicted in red) is transmitted by *Spissistilus festinus*, the three-cornered alfalfa hopper, in a circulative, nonpropagative mode. In the virus acquisition phase, *S. festinus* ingests GRBV through the food canal while feeding on the phloem of an infected grapevine, and the virus travels into the gut (depicted in blue), where it crosses from the gut lumen to the hemolymph and then into the salivary glands (depicted in purple). Only after entering the salivary glands is the virus considered acquired by the insect. In the inoculation phase, GRBV is transmitted into a new grapevine via the salivary canal when *S. festinus* feeds. The time between *S. festinus* initial ingestion of GRBV and successful transmission into a new host (i.e., acquisition access period) is 10 days.



in the greenhouse (12, 52, 61, 62, 66, 82, 83), but the capacity of most of these hemipterans to transfer the virus from an infected donor plant to a healthy recipient plant is unsettled (80). The confusion surrounding an unequivocal identification of insect vectors of GRBV is due to the investigation of vector candidates that are not phloem-feeders, transmission assays that are not replicated or use a suboptimal acquisition access period (AAP), thus creating situations for which it is impossible to independently validate the findings (80).

A significant co-occurrence and covariation between the spatial distribution of GRBV-infected vines in a diseased vineyard and viruliferous specimens of *S. festinus*, a phloem-feeder, was initially described in 2018 (54). This association suggested that this treehopper is likely a GRBV vector of epidemiological relevance. Thus far, it is the only proven arthropod vector of GRBV, with a documented presence of the virus in the salivary glands (61, 81) and replicated transmission assays in the greenhouse (61, 62) and in the vineyard (66). A circulative, nonpropagative transmission of GRBV by *S. festinus* with a 10-day AAP on infected grapevines was reported (**Figure 3**) (61). This AAP is very long compared with that of other geminiviruses (74, 76). Transmission is transstadial (61) but not transovarial (84). GRBV is not transmitted vertically through seeds (61). Therefore, transmission occurs vertically through vegetative propagation and horizontally via *S. festinus*.

Overall, transmission of GRBV by *S. festinus* is inefficient between wine grape cultivars in the greenhouse (4–42%) (61, 62, 85) and in the vineyard (2–10%) (66). Interestingly, the plant species used as virus donor or as virus recipient in transmission assays influences the rate of transmission (61, 62). These results suggested that transmission could be associated with a distinct behavior of *S. festinus* on different plant species. Among the other vector candidates of GRBV described in the literature (12, 82, 83), no information is available on the presence of GRBV in the salivary glands, and transmission experiments have not been replicated, casting doubt on their validity or requiring additional experiments to confirm the findings.

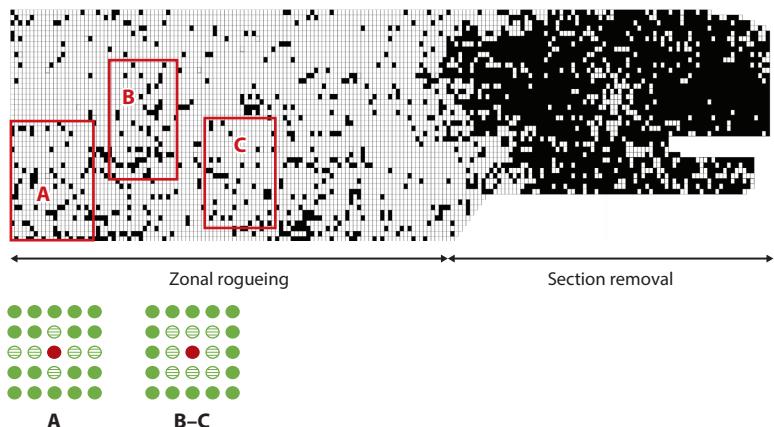
Transmission assays of GRBV by *S. festinus* have been thoroughly described with *Vitis* species, the natural hosts of the virus, in the laboratory and in the vineyard, and with snap bean, an experimental pseudosystemic herbaceous host of the virus (80). These detailed protocols should help the design and implementation of optimal transmission assays by researchers interested in GRBV transmission. They are also anticipated to alleviate some of the confusion related to vector biology and transmission biology regarding GRBV.

DISEASE MANAGEMENT

Prevention is the cornerstone of plant viral disease management, particularly when no sources of resistance are known, as is the case for GRBV in *Vitis* species. Therefore, due to the demonstrated importance of GRBV to the grape and wine industries, GRBV has been included in clean plant programs and state certification programs throughout North America. These actions are essential for reducing the presence of GRBV in the propagation material and planting stocks. Consequently, when clean, certified planting stocks are selected by growers, the level of virus inoculum is limited when new vineyards are established, and the rate of secondary spread is substantially reduced.

In diseased vineyards, rogueing is used to reduce the virus inoculum and limit secondary spread. Rogueing consists of scouting vineyards, mapping diseased vines, removing diseased vines, and replacing them with clean vines. In California, symptomatic vines are typically flagged after harvest, and some are tested for viruses to validate the occurrence of GRBV. Then, flagged vines are removed in the winter and replaced with clean, certified vines. Rogueing when GRBV incidence is low was associated with slower spread in Oregon vineyards (59), supporting the cutoff value of less than 30% disease prevalence as an economically sound disease management option (**Figure 4**) (51). In British Columbia, Canada, rogueing was effective in reducing GRBV



**Figure 4**

Managing secondary spread of grapevine red blotch virus (GRBV) may be necessary in areas where the vector, *Spissistilus festinus*, is active in vineyards. Depending on the incidence and spatial distribution of GRBV-infected grapevines, it is recommended to either remove the entire vineyard or a section of the vineyard (*top right*) or rogue infected vines and neighboring vines (*top left*). Vineyard removal or vineyard section removal are recommended when disease prevalence is higher than 30%. When prevalence is less than 30%, zonal rogueing, or the removal of a diseased vine and neighboring vines, is recommended. Zonal rogueing of six vines (one on each side of a diseased vine and two vines across two rows; *hatched green dots*) surrounding a single diseased vine (*red dot*) should be removed in areas where disease incidence is less than 20% and infected vines (symptomatic and asymptomatic) are aggregated (area A). In areas B and C, where disease incidence is less than 20% and infected vines are not aggregated, zonal rogueing of eight vines (*hatched green dots*) immediately surrounding the single diseased vine (*red dot*) is recommended. In summary, a zonal rogueing strategy of seven or nine vines is recommended to manage GRBV. Figure adapted from Reference 67.

incidence in several vineyards where detection of new infections was minimal and *S. festinus* is not present (86). Rogueing efforts have been implemented in northern California vineyards where *S. festinus* is active, but it is not yet clear how effective rogueing practices are at managing red blotch disease. Rogueing can be challenging for a perennial fruit crop such as grapevine because young replacement vines require more water and nutrients to grow than established, mature vines. In addition, they will not be productive for two or three growing seasons, and their fruits have less concentrated flavors, lower complexity, and poor character compared with fruits from mature vines. These intrinsic factors related to the grapevine create complexities in the adoption of rogueing as a red blotch disease management response.

Given regional variability in red blotch disease ecology and epidemiology, disease management programs necessitate tailoring to specific regions, specific vineyards, and even specific zones within vineyards based on patterns of aggregation of infected vines (**Figure 4**). Therefore, zonal rogueing or the targeted removal of a diseased vine and several surrounding vines, regardless of whether they display disease symptoms or not, has been devised as a novel disease management response to accommodate symptomless infections and the aggregation level of infected vines (**Figure 4**).

GRBV has highlighted the concepts of triangulation and replication in the ability to develop strategies for disease management based on ecological data. For example, pairing spatiotemporal statistics to illustrate GRBV spread over time with genotyping of GRBV isolates in infected vines provided multiple lines of evidence to reveal the dynamics of virus spread. Similarly, although GRBV is transmitted more efficiently by the southeastern than the western genotype of *S. festinus* in controlled experiments (85), ecological data in a vineyard in the southeastern United



States suggest that GRBV spread in vineyards is nonexistent or incredibly slow (E. Cieniewicz, unpublished data). This is likely because *S. festinus* has access to plenty of preferred, non-*Vitis* feeding hosts in Georgia vineyard ecosystems compared to in northern California. Providing multiple lines of evidence, particularly regarding ecological data, is critical to draw appropriate conclusions and formulate management strategies that resonate with growers.

DISEASE MITIGATION

Viticulture practices, such as sequential harvest and supplemental irrigation, and winemaking techniques such as chaptalization have been explored in an effort to mitigate the effects of GRBV on berry and/or wine quality. Most of these efforts have proven ineffective (46, 87, 88) because the effects of GRBV on vine and berry metabolism are not limited to a single metabolic pathway. Moreover, although mitigation efforts might be desired by winemakers in some regions where GRBV is not spreading, they are a band-aid approach with negative long-term consequences. Mitigation efforts may provide some perceived profitability in the short term, but they fail to address the root of the problem, which is the persistence of the virus inoculum in vineyards. We argue that mitigation practices are not likely to improve the red blotch disease situation and may exacerbate it by encouraging persistence of the virus inoculum that may facilitate secondary spread in vineyards. The effectiveness of mitigation practices likely will also vary by cultivar, vineyard site, and season. Therefore, promoting these practices might also create confusion among the winemaking and grower communities.

SOCIAL EFFECTS OF THE DISEASE

Red blotch disease likely emerged a long time ago (36) but was recognized only 20 or so years ago by grower communities. Since the first description of disease symptoms in 2008, substantial progress has been made on disease biology, diagnostics, transmission biology, and disease ecology. In addition, Koch's postulates were fulfilled, a remarkable accomplishment for a newly described virus of a perennial fruit crop, documenting GRBV as a causal agent of red blotch disease. However, beyond research accomplishments, the biggest achievement related to the discovery of the virus was its unprecedented capacity to create opportunities for all the players of the grape and wine industries—including growers, vineyard managers, wineries, nurseries, researchers, extension educators, regulators, policymakers, private testing laboratories, and consultants—to interact. This offered new possibilities to collectively discuss and address the threats caused by a recently identified viral disease. Extensive communications among all members of the grape and wine industries focused on disease biology, GRBV detection, disease spread, disease management, and research priorities.

From a historical perspective, communication has never been so efficient and constructive within the grape and wine industries, with growers spearheading educational efforts and seeking change. As a result, GRBV was included in state certification programs in the United States. Nurseries destroyed their G2 increase vineyards (or base vineyards) and established new ones with GRBV-free stocks at new sites. In addition, some G1 vineyards (or initial vineyards) were destroyed and/or moved to greenhouses and the GRBV status of G2 vineyard blocks (or increase vineyards) is monitored annually by nurseries, independently of the surveys carried out by inspectors of the local departments of agriculture in the frame of a certification program. These are drastic changes. Moreover, growers themselves are testing the GRBV status of G2 vines managed by nurseries prior to either ordering grafted vines or accepting planting stocks. This can only be achieved because of a mutual openness from both the nurseries and growers and a goal to ensure the cleanliness of the planting stocks. Finally, red blotch disease was included in the priorities



of the California Department of Food and Agriculture Pierce's Disease/Glassy Winged Sharpshooter research program. These unprecedented efforts have funded research on GRBV and have undoubtedly brought all the actors closer together, thanks to grower communities creating opportunities for a sustained dialogue (**Figure 1**). Nonetheless, this level of communication within the grape and wine industries underscored the need for further improvements in all the production steps of clean planting stocks. Time will tell if future modifications curtail the effects of red blotch disease.

DISEASE ECOLOGY: LESSONS LEARNED FOR MEANINGFUL COMMUNICATION

Great strides have been made on disease ecology, albeit with a good deal of initial distraction. Indeed, the misidentification of arthropod vectors of GRBV generated lots of confusion. The major sources of confusion have been identified, and ways to address them have been outlined in an opinion piece (80). More importantly, the confusion on GRBV transmission has substantially delayed the development of sound red blotch disease management strategies. Therefore, it is not too surprising that a deficit of reliable information on red blotch disease ecology has been identified as a major limiting factor for the adoption of disease management practices by grower communities (89). Misinformation on potential vectors of GRBV convinced some grape growers and vineyard managers to change their pest management practices because they were compelled to use pesticides and adopt new cultural practices, and they thus invested additional financial resources, unfortunately against unproven insect vectors.

Disseminating information on research findings to grower communities through various educational methods is critical to demonstrate the genuine desire of the scientific community to address real-world problems. Communication with growers needs to be rooted in solid, science-based information rather than on preliminary data that have not been validated internally and/or independently. Although virus disease management strategies are relatively simple conceptually, they have been overall poorly adopted in vineyards, as previously discussed (90). Briefly, the futility of chemicals to combat viruses, the seasonal variability of virus effects, the high costs of rogueing, and a lack of reliable sources of information are some of the factors that contribute to uncertainties and overall low adoption levels of disease management responses (90). Remaining authentic and upholding integrity and ethics are essential to establish and maintain relationships with grower communities. These efforts also pay off for researchers, who are more likely to be granted access to grower properties for research purposes when trust is established and nurtured.

FUTURE RESEARCH PRIORITIES

Research on GRBV should address several outstanding questions and will likely also raise new questions. Twelve open questions about GRBV were recently listed by Krenz et al. (91), including questions related to other viruses and vectors involved in disease etiology and epidemiology, transmission biology, mechanisms of disease development, gaps in GRBV ecology, and management and diagnosis. Improvements in GRBV detection will undoubtedly elevate both research capacity and management strategies. Remote sensing using aircraft or satellites to detect GRBV-induced changes to grapevines has potential for usage in large-scale epidemiology studies, applications for virus detection in clean plant programs and nurseries, and early intervention to reduce virus inoculum in vineyards. Similarly, detection assays are currently limited to DNA-based methodologies. The availability of a specific antibody would allow for development of serological assays that may be easier to scale up for use in certification programs. Although LAMP has been developed and adopted, to our knowledge, this method is being widely used only in northern California.



Decision support systems have been developed for some other vector-borne viruses (92–95) and might be useful in aiding decision-making in, for example, vineyard rogueing practices. Canine detection of viruses is gaining popularity for the detection of bacterial and viral pathogens (96, 97), but its potential for grapevine viruses, including GRBV, is still unknown. There is also a need for improvement in options for growers to get their vines tested for GRBV and other viruses by private laboratories. Uncertainty within the grower community on which testing providers to trust and questions regarding the validity of test results can prevent timely management actions.

Despite substantial progress in understanding GRBV transmission by *S. festinus*, there are still remaining questions about transmission biology. At this point, only *S. festinus* has been proven as a bona fide vector. It is important to determine if there are any other vectors because even inefficient or infrequent vectors can substantially exacerbate disease spread. Most of the research on GRBV transmission ecology has thus far been performed in northern California and southern Oregon, and therefore expanding this research to other regions where secondary spread may occur is important for devising regionally relevant management strategies. Determining how climate change is affecting and will affect GRBV and vector distributions and behaviors is important to develop measures for mitigating potential new epidemics. Although it is challenging to predict how climate change will affect red blotch disease on a systems scale, areas with a high density of wine grape production—e.g., the Central Valley, Sonoma, and Napa Valley in California—may benefit from area-wide management programs that are in practice for controlling other vector-borne pathogens of grapevine (98), citrus (99, 100), and tomato (101).

One area requiring further research is understanding basic GRBV biology. GRBV and other grabloviruses form a new group of viruses, and although there is some homology with other geminiviruses, GRBV biology is not well-characterized yet. Visualization of viral particles has never been reported, and few studies have addressed GRBV genome expression (10, 15). More information is needed on mechanisms of viral genome expression and replication and virus-host interactions. It is important to determine how GRBV behaves in mixed infections with other viruses and other pathogens of grapevine, considering it does induce a defense response in grapevine (102). It is unclear if GRBV modulates vector behavior to encourage its own dispersal, i.e., vector manipulation, as has been observed for numerous other vector-borne viruses (103, 104). Unknown mechanisms underlying tripartite virus-vector-host interactions represent enticing opportunities for future research.

CONCLUDING REMARKS

Despite much progress since the discovery of red blotch disease and its causal agent, many questions remain unanswered regarding GRBV biology, ecology, and optimal management strategies. Triangulated approaches with robust experimental replication are needed to address the most pressing problems associated with GRBV. Despite the many biological challenges associated with GRBV, this virus has transformed the interactions among the different players of the grape and wine industries, with grower-led initiatives and priorities guiding the research. As an example, the California Department of Food and Agriculture Pierce's Disease/Glassy-Winged Sharpshooter Board, which is composed of representatives from the wine grape industry, sought support from the National Academies of Sciences, Engineering, and Medicine to conduct a consensus study on red blotch and leafroll diseases. This grower-initiated request for a science-based review of grapevine virus research and disease management demonstrates the importance of GRBV research to the grower community (105). GRBV research has also offered opportunities for training students in plant virology and uncovering some of the intricacies of an unprecedented pathosystem.



We are optimistic regarding the future of GRBV research and the potential for developing and implementing science-based red blotch disease management practices in vineyards.

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The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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