Recent Progress in Understanding of Virus Pathogens that Affect Grapevines

James A. Stamp, Ph.D.

As Wild and Weedy grapevines have evolved so have viruses that benefited either pathogenically or benignly from their relationship with the plants.

It is only comparatively recently, however, that our knowledge of virus biology, realized in tandem with the development of new detection methods, has permitted rapid, efficient and accurate detection of the submicroscopic particles—ribonucleic acid (RNA) sheathed in a protein coat—that cause the various virus-associated diseases.

This article summarizes currently available information that will be of interest to growers concerned with the rapid spread of leafroll disease and unsure of the significance of recently discovered viruses.

Viruses are generally transmitted by insect or nematode vectors and through propagation practices. Pearson and Goheen, in their 1988 APS Press publication Compendium of Grape Diseases, suspected that closteroviruses were the cause of leafroll disease but could not report conclusive evidence of cause and effect. Substantial progress has been made since 1988; and now we understand, for example, that there are at least 10 defined species of leafroll virus and that Grapevine Leafroll-associated Virus-3 (GLRaV-3) has at least seven genetically-defined variants.

Consequently, improved virus detection techniques over the past two decades have resulted in the ability to more accurately detect certain known viruses and the ability to identify and detect previously unknown viruses.

The availability of this improved detection technology coincided with the rejection of AXR#1 rootstock, the widespread adoption of previously untried-in-California rootstocks and the introduction to California of a wide array of European varietal clones, many of which were contaminated with economically important viruses.

Evolutionary Relationship Between Viruses and Insect Vectors

Grapevine viruses are transmitted by insect or nematode vectors. Grapevine Fanleaf virus is a nepovirus and, as such, is vectored by the nematode Xiphinema index. This nematode and virus complex are devastating to viticulture, especially in the Napa Valley region around Rutherford, California, where viticultural practice is determined by their presence.

Specifically, only one rootstock variety, VR039-16, a University of California-developed hybrid, provides resistance against transmission of fanleaf virus from the nematode to the fruiting variety. VR039-16 is extremely vigorous and highly susceptible to crown gall, but there are no alternative remedies for dealing with this disease complex. Currently, California nurseries are sold out of VR039-16 stock for all but green vines to be delivered in spring 2013.

Several leafroll virus strains are vectored by insects. Just as viruses have evolved alongside grapevines, so have insect vectors evolved with the viruses they transmit. A very interesting 2010 study (Tsai et al.) examined the phylogenetic relationship between different leafroll strains, along with other non-grapevine members of the Closteroviridae virus family, including tomato and citrus pathogens and the various insect pathogens known to vector them. Within the Closteroviridae family it has been shown that members of the genus Closterovirus are aphid-borne, ampoloviruses are mealybug and soft scale-borne, and criniviruses are transmitted by whiteflies (Figure 1).

Figure 1 (Tsai et al.) shows putative vectors (black sub-branches) of various grapevine and non-grapevine viruses (e.g., because it is a crinivirus, GLRaV-7 should be vectored by whiteflies) and known vectors (colored branches) of others. For example, GLRaV-1, -3, -4, -5 and -9 are now known to be vectored by mealybugs (GLRaV-4 and -9 reported for first time in the Tsai et al, 2010 article); and because GLRaV-6, -10 and -11 are also ampeloviruses, it is suspected that these, too, should be vectored by mealybugs, although this has not been proven.

Similarly, as GLRaV-2 is a closterovirus, it should be vectored by aphids although not proven to date. The authors were unable to find evidence of mealybug-vector specificity and noted that different mealybug species transmitted GLRaV-3 while one species, Planococcus ficus (vine mealybug), transmitted five different GLRaVs.
Recently Detected Viruses of Interest

**RUPESTRIS STEM PITTING VIRUS SYRAH STRAIN**

Rupestris Stem Pitting virus Syrah strain (RSP-Syrah) was first isolated by Dr. Adib Rhowani’s research group at Foundation Plant Services, UC Davis in 2005. RSP is a species of virus, and RSP-Syrah is a strain or genetic variant of this virus species. RSP-Syrah was isolated from a Syrah vine that exhibited symptoms of “Syrah Decline” in a California vineyard. Since then, RSP-Syrah has been detected in approximately 50 percent of all rootstock and scion materials tested by this author (sideBar 1).

### SIDE BAR 1: Clones and Rootstocks Contaminated with RSP-Syrah

Many of the newly released ENTAV scion clones have tested positive for RSP-Syrah, including Cot 596, Petite Verdot 1058, Pinot Noir 943, Pinot Noir 115, Merlot 343, Syrah 470 and Cabernet Sauvignon 685. Tested California field selections, such as Pinot Noir Calera, Chardonnay Wente and Sauvignon Musque, and CDFA-certified FPS selections, such as Chardonnay 17 (Robert Young) and Riesling 17, have also tested positive for RSP-Syrah. CDFA-certified rootstock increase block varieties testing positive for RSP-Syrah include: 3309C, 1616C and VR 039-16. Not all sources of these rootstocks have tested positive for RSP-Syrah—it is possible to find rootstock blocks negative for this virus. On the other hand, recent re-testing of previously negative blocks has turned up positive vines (sideBar 2).
Dr. Adib Rhowani of UC Davis recently confirmed that there is no known correlation (cause and effect) between the presence of RSP-Syrah and vine decline in grapevines. To state that such a correlation existed would require that RSP-Syrah be the only contaminant in a grapevine plant—requiring absence of all viruses, detectable and undetectable—and that other biotic and mechanical factors were not at work, such as fungal pathogens, site/terroir issues, plant material issues, i.e., imperfect graft unions, etc. Laboratory analysis notes that suggest a correlation exists between contamination by RSP-Syrah and vine decline should be read with skepticism.

**Sidebar 2: Challenges in Detecting RSP-Syrah**

Virus testing of Cabernet Sauvignon ENTAV 169 illustrates the difficulty in detecting RSP-Syrah in grapevine stock. In November 2008, five CS169 increase block vines tested negative for RSP-Syrah at Lab 1. In November 2010, duplicate samples from six adjacent vines (derived from the same FPS parent source vines) tested positive for RSP-Syrah at Lab 1 but negative at Lab 2. Left and right cordon samples submitted to Lab 3 from two of the five vines tested in 2008 tested positive and negative, respectively, in December 2010. Left and right cordon samples submitted in December 2010 to Lab 4 from two of the six positive vines tested in November 2010 were both RSP-Syrah positive from one vine and both negative from the other. When Lab 1 isolated new extracts from the cuttings submitted in November 2010, one of six was negative for RSP-Syrah. These observations suggest that RSP-Syrah is quite unevenly distributed within the vine and raise concerns about the accuracy of the test offered by commercial laboratories.

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**Grapevine Syrah Virus-1**

Grapevine Syrah Virus-1 (GSV1) was isolated and characterized from a Syrah vine showing symptoms of Syrah decline. The virus was also isolated from symptomless wild Vitis species. Rhowani recently confirmed (personal communication) that there is no evidence to suggest that this virus is correlated with Syrah decline or any type of vine decline. GSV1 is most closely related to Grapevine Fleck virus. Fleck is a ubiquitous virus that is not regulated by the CDFA nursery certification program. Approximately 10 percent of all rootstock and scion increase blocks tested by Stamp Associates, since the 2009 availability of a lab diagnostic procedure, have proven positive for GSV1.

**Grapevine Leafroll Associated Virus 2 Red Globe**

In California, a novel closterovirus was detected in a Redglobe grapevine associated with graft incompatibility and named Grapevine Leafroll-associated virus-2 Redglobe (GLRaV-2RG). When asymptomatic, GLRaV-2RG-infected Redglobe scion buds were graft-inoculated onto Cabernet Sauvignon indicator plants—grafted to 18 different rootstocks—it proved lethal on 1616C, 5BB, 5C and 3309C.

In contrast, standard GLRaV-2 virus-inoculated plants produced only typical leafroll symptoms. Sequencing of double-stranded RNA from infected Redglobe grapevines showed that GLRaV-2RG was most closely related to GLRaV-2 (Alkowni et al., 2011). It is assumed that the virus is not widespread as the author has not detected GLRaV-2RG in any certified or non-certified vines to date. A 2003 Italian survey for this virus in about 380 accessions of table and winegrape varieties proved that GLRaV-2RG was present in other table grape varieties apart from Redglobe, though to a lesser extent, while it was not detected in wine varieties (Angelini et al., 2003).

**Grapevine Leafroll Associated Virus Carnelian Strain**

Carnelian is a leafroll virus associated with mild symptoms of the disease, including moderate downward rolling and premature interveinal reddening. Symptoms that resemble leafroll disease were observed on grapevine cultivar Carnelian specimens growing at UC Davis. The presence of leafroll infection was confirmed by grafting onto the leafroll-specific indicator Cabernet Franc. The source plant tested negative for all known grapevine leafroll-associated viruses by ELISA and RT-PCR. Preliminary analyses have shown a close relationship between Carnelian and GLRaVs-4, -5, -6 and -9 (Abou-Ghanem-Sabanadzovic, et al., 2008). Diagnostic procedures for this virus have only very recently become available.

**Leafroll Species and Genetic Variants**

Recent work by Dr. Rodrigo Almeida of UC Berkeley tracked populations of different leafroll species in a study of 36 Napa Valley vineyards and demonstrated the existence of at least seven genetically distinct variants of GLRaV-3 (Sharma et al., 2011). Phylogenetic analysis demonstrated that three GLRaV-3 variants represented 71 percent of all GLRaV-3 positive samples in the Napa study.

It seems that the variants, in general, are sufficiently similar to be detectible by standard PCR techniques although it is not known whether ELISA can detect GLRaV-3 variants. There is some evidence, however, that specific variants may be undetectable with standard techniques, which could help explain the many instances of leafroll symptom development where lab analyses fail to detect the virus. Almeida’s work showed that GLRaV-3 is the dominant leafroll species in Napa (Figure 2). Work in Europe has demonstrated the existence of variants of GLRaV-2, some of which are biologically distinct. It should be expected that variants of other GLRaV strains exist, too (Almeida, personal communication).
Virus Detection Techniques and Sampling Strategies

Most laboratories that handle grapevine tissue samples use ELISA in combination with PCR to detect economically important viruses. With the exception of nepoviruses (for example, grapevine fanleaf virus and tomato ringspot virus)—best diagnosed in fleshy shoot tips in early spring—the remaining viruses of greatest concern to growers are detected most readily in basal leaves and mature cane tissues from mid-September through budbreak.

The gold standard for determining the presence of a virus is the grafting of a bud from a suspect-infected plant onto an indicator plant that readily expresses symptoms of the disease. Cabernet Franc is the indicator for leafroll disease. An in-house analysis of data from 100 plants with LR symptoms, collected over five years and testing positive for GLRaV-2 and/or GLRaV-3, illustrates the generally accepted differential sensitivity of alternative rapid diagnostic techniques in comparison to the indicator system (Table 1, Vicki Klaassen, FPS, UC Davis).

Table 1: Sensitivity of diagnostic procedures: Five years of test data GLRaV-2 and -3

<table>
<thead>
<tr>
<th></th>
<th>GLRaV-2</th>
<th>GLRaV-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cabernet Franc Woody Index</td>
<td>POS 100%</td>
<td>100%</td>
</tr>
<tr>
<td>Real-time RT-PCR</td>
<td>POS 97%</td>
<td>98%</td>
</tr>
<tr>
<td>RT-PCR</td>
<td>POS 79%</td>
<td>97%</td>
</tr>
<tr>
<td>ELISA</td>
<td>POS 29%</td>
<td>67%</td>
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</table>

n=100. With permission, Dr. Vicki Klaassen, FPS, UC Davis

Klaassen cautioned that the data presented in Table 1 are very specific to FPS antisera and samples but do serve to illustrate a general trend in sensitivity between the different methods. The data are a measure of diagnostic sensitivity and shows that in the case of GLRaV-2, for example, the FPS ELISA test detected the virus 29 percent of the time that it was present, compared to 79 percent and 97 percent for RT-PCR and Real-time RT-PCR, respectively.
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Private testing of increase blocks is an expensive proposition. Including set-up fees, it costs approximately $350 to test one sample for a range of viruses, including several leafroll-associated viruses, vitiviruses A, B and D, Rupesstris Stem Pitting virus and the Syrah variant, etc. Because of these financial constraints, vineyards are sampled in an effort to gauge the virus status of the block without testing every plant.

Knowledge of the source of the vines in the block is critical. If all vines are derived from a single foundation plant, this should rule out variability resulting from propagation from vines of different virus status. The next critical step in the process is field evaluation. This really does not apply to rootstock increase blocks as vines rarely show symptoms of virus disease. However, annual field examination of scion increase blocks is essential so that questionable sources can be ruled out before spending on lab diagnostics. In preparation for a new planting, knowledge of intended rootstock and rootstock on which potential budwood supplies are growing is also helpful.

Generally, when collecting samples from a single vine, tissues should be collected that reflect the general habit and size of the plant. If sampling from an established bi-cordoned vine, three cane cuttings from each cordon would represent the ideal amount of tissue required for analysis. If working...
with a laboratory that uses Real-time RT-PCR, there is more flexibility in sample collection and a greater opportunity to composite samples, that is, place tissues from two vines into one sample, thereby doubling the number of vines tested for a fixed budget. Compositing samples, however, presents a fairly delicate balance of risk versus reward. Multi-seasonal field examinations, familiarity with propagation history, the surrounding habitat and the size of vine should all be considered.

Lastly, it is important to weigh the expertise of the selected laboratory. An extensive series of comparative “replicate” analyses conducted during the winter 2011/12 season highlighted significant differences in outcome between laboratories (expected outcome from control samples), including sensitivity, cost and turn-around time.

**SIDEBAR 3: Rapid Field Use Diagnostic Kits: Are They in Our Future?**

There is a vision that some day a grower will walk into a vineyard, collect a tissue sample and understand the virus status of a plant within a few minutes. Rapid diagnostic testing is now routinely available in the field of human medicine but is still a distant promise for grapevine applications.

According to Dr. Alan Wei, AgriAnalysis, West Sacramento, California: “Field use diagnostic devices would allow PCAs, consultants and growers to take a leaf or cane sample and conduct a diagnostics test in the field. ‘Sample-to-result’ would take a few minutes. The most notable such device is the dipstick test strip based on immunoassay technology using highly specific antibodies. Such tests are widely used in medical diagnostic screening and are also available for some plant pathogens. However, the current color-based dipstick tests are not sensitive enough for early virus detection and are prone to false positive results, in part due to the homogenous nature of plant samples.

“Instrument-based tests, which use high sensitivity fluorescent dyes or luminescent indicators, are still in development stage. Given the large number of pathogens affecting grapevines, ranging from viruses, bacteria, fungi and mycoplasma, it is unlikely that one device will measure all pathogens at once. However, devices that can allow for the detection of certain key indicator grapevine pathogens, such as leafroll virus 3, fanleaf virus and Pierce’s Disease, will likely be the first to hit the market in the next five to 10 years. The cost of such a device should be $1,000 to $2,000, and each test should be around $5 to $10. As is true for any consumable product, the driving factor for price is volume.”

**Status of CDFA-Certified Increase Block Planting Materials**

Extensive testing of CDFA-certified increase blocks has revealed that many rootstock sources are contaminated with economically important viruses (Stamp, 2010). A list of removed and virus-contaminated increase block sources was requested from the CDFA but was unavailable at the time of publication. Recent CDFA-certified increase blocks that test positive for various economically important viruses are listed in **SIDEBAR 4**.
**SIDEBAR 4: Recently Detected Leafroll and Other Viruses in CDFA-Certified Increase Blocks**

The following varieties and clones were recently found to be contaminated:

- Cabernet Franc FPS 01: GVA
- Petite Sirah (Durif) FPS 03: GLRaV-3
- Pinot Noir FPS 97 (Swan): GLRaV-3
- Riesling FPS 17: GLRaV-3, Grapevine vitivirus A (GVA)
- Sauvignon Blanc FPS 01: GLRaV-3

**Preliminary Results on the Effect of Viruses on Rootstock Health**

Although growers and researchers are much better informed about the relationship between insect vectors and leafroll, there has been little work devoted to understanding the interaction between different virus strains and rootstock health. Work underway by Rhowani and co-workers, although preliminary, has shown a differential response from a series of nine rootstocks grafted to Cabernet Franc and inoculated by rootstock budding with known virus isolates.

Vines are currently planted in a field trial at UC Davis. Symptoms that developed on the field-grown inoculated Cabernet Franc/rootstock vines were assessed on a five-point scale, ranging from “0,” no symptoms, to “4,” where the whole plant was affected by symptoms. Vines that turned completely red, often with shortened internodes, frequently died and were classified as “4R.” It is suspected that these vines had died or would soon die because of graft union or rootstock failure, resulting from virus activity.

Preliminary results are presented in **FIGURE 4** and summarized in **SIDEBAR 5**. Results are based on the reaction of inoculated vines during their first two years of vineyard growth. The results are expressed as the extent of leafroll symptom development (0-4R) in the Cabernet Franc vines grafted to the nine different rootstocks (**FIGURE 4**).

**SIDEBAR 5: Preliminary Data on the Effect of Leafroll Associated Viruses on Symptom Development in Inoculated Cabernet Franc Vines Grafted to Nine Rootstocks**

1. The combination of GLRaV-1 and GVA was lethal to vines grafted to 420A, Freedom, 3309C and 101-14MG rootstocks.
2. GLRaV-2 virus isolates induced severely adverse effects on Freedom and SBB rootstocks, and it was expected that vines would die in the following season.
3. Most severe, but non-lethal, symptoms were observed with GLRaV-1, -2 and -3 inoculations.
4. Least severe symptoms were observed with GLRaV-4, -5 and -9 inoculations.
5. Inoculations with GLRaV-7 failed to induce symptom development on the Cabernet Franc indicator plants.

**FIGURE 4**

Effect of different viruses on symptom expression in Cabernet Franc indicator vines grafted to nine different rootstocks

<table>
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<tr>
<th>Isolate</th>
<th>Virus</th>
<th>420A</th>
<th>Frdm</th>
<th>3309C</th>
<th>101-14MG</th>
<th>St. G. 18</th>
<th>St. G. 15</th>
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**Virus Transmission, Sanitation and Regional Disease Control Strategies**

Evidence suggests that the main source of leafroll spread is through insect vectors and/or propagation materials (Stamp, 2010). There is no evidence that in-field root grafting or seasonal pruning activities are a source of transmission. It is possible, however, that pruning shears could move the virus from an infected to a non-infected sample.

Recent Detection of Leafroll and Other Viruses in CDFA-Certified Increase Blocks

- **Figure 5** shows the development of a GLRaV-3 infection, originating at avenue end-post vines and spreading along the rows. A new vineyard planted on the other side of the avenue soon became contaminated with GLRaV-3.

- Undertake routine seasonal operations in infected blocks after working in clean blocks.

- If possible, maintain separate equipment pools for infected blocks.

- Wash down and remove soil and vegetation from equipment and vehicles moved from infected blocks.

- As a general precaution, control movement of vehicles and equipment into all vineyard blocks. Establish “no go” areas out-of-bounds to all but approved equipment and personnel. This is especially important when blocks are under development adjacent to established vineyards. Consider that contractors and laborers are visiting your property immediately before or after visiting another vineyard.

- Figure 5 shows the development of a GLRaV-3 infection, originating at avenue end-post vines and spreading along the rows. A new vineyard planted on the other side of the avenue soon became contaminated with GLRaV-3.
Detection and chemical controls, in combination with good sanitation practices, are critical for the control of mealybug populations. A range of chemical tools is available that offers effective control. Strategies for their use should consider mealybug species, age of vineyard and neighboring vineyards, treatment of new blocks and established blocks, and removal of individual contaminated vines and whole blocks. Mating disruption methods may also prove beneficial for the control of mealybug populations.

For an in-depth discussion of chemical and mating disruption technologies, along with a discussion of the potential of regional and community approaches to controlling mealybugs and leafroll disease (SIDE BAR 6), see the presentations by Kent M. Daane, UC Berkeley (Insecticide controls for mealybug pests: impact as a control for grape leafroll and other pest issues) and Neil McRoberts, UC Davis (Epidemiological analyses of leafroll diseases: Current understanding and future prospects) delivered at the UC Davis “Wine and Wine Grape Research 2012” presentation (February 14, 2012) (http://ucanr.org/sites/intvit/?uid=281&ds=351).

FIGURE 5 (photo below)
GLRaV-3 is seen in an established Rutherford vineyard, with the virus apparently moving from infected end post vines into rows.

JAMES A. STAMP

SIDE BAR 6: Developing Regional Strategies for Leafroll Control
It is becoming clear that leafroll and virus disease are a community problem—not just one that individual growers can or should try to tackle on their own. This is all the more obvious when one considers the prospect of replanting an infected block that is surrounded by diseased vineyards. Development of regional strategies for monitoring and dealing with the problem makes good sense. This work is being spearheaded by a group of UC researchers and, although in its infancy, offers real hope for a rational and livable solution to a problem that is steadily getting worse.

According to Neil McRoberts, Department of Plant Pathology, UC Davis: “The work on regional/neighborhood group/area-wide control is at an early stage. We know from the fact that leafroll is spreading that individual efforts are not working and also from experience with other pests in other crops that area-wide management can benefit growers if enough people practice it.

“On the other hand, it’s a big change in culture for groups of individualists to start cooperating and sharing information, so it’s easy to understand why the idea of neighborhood groups is taking a while to get going. Trust comes into play in two ways. First, in terms of the trust that is required among the growers right now to share sensitive information, but also trust on their part individually and collectively that cooperating will bring benefits in the future. Gambling on an uncertain future pay-off is never an easy thing to do. The whole UC team, though, are working on this idea of getting more cooperation going among growers.”
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Conclusion
It is exciting to learn of recent progress and new strategies that are under development by UC staff designed to further our understanding of various grapevine virus diseases. Given that leafroll disease is rapidly becoming a serious statewide issue and that both insect vectors and contaminated propagation materials are involved, it is at least slightly comforting to acknowledge that California has a team of highly skilled researchers dedicated to understanding and ultimately fixing the problem.

It seems clear that, as with other fleeting pests, sanitation practices are key to control and that looking at the bigger picture, through development of community and regional strategies, is going to play a very significant role as we attempt to rein in leafroll disease. New viruses are being discovered regularly, but it seems that our old favorite, leafroll, is still the one to be concerned about. In the meantime, implementing common sense approaches to viticulture, based on preventative measures—be it sanitation practices or careful selection of nursery stock—must be at the top of the growers toolkit.

References


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