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REVIEW

Grapevine viruses: a multitude of diverse species with simple but overall poorly adopted management solutions in the vineyard

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Abstract

Eighty-six viruses have been isolated to date from grapevines worldwide. Some of these viruses are associated with economically damaging diseases such as leaf mottling and deformation, vein clearing, leafroll, degeneration and red blotch. They belong to the families *Betaflexiviridae*, *Caulimoviridae*, *Closteroviridae*, *Secoviridae* and *Geminiviridae*, and are transmitted by diverse vectors such as mealybugs (Hemiptera: Pseudococcidae), soft scale insects (Hemiptera: Coccidae), an aphid (Hemiptera: Aphididae), dagger nematodes (Nematoda: Longidoridae), a treehopper (Hemiptera: Membracidae) and eriophyid mites (Acari: Eriophyidae). Management of these viruses primarily relies on preventive measures to limit their presence in the propagation and planting material. In the vineyard, specific disease scenario-based strategies such as rogueing in combination with agrochemical applications to limit vector populations, if appropriate, and the removal of entire parcels and their replacement with clean planting material, including vector tolerant rootstocks, if opportune, are implemented to reduce their incidence, prevent their spread and mitigate their impact. These solutions are simple but their implementation is often suboptimal and their adoption is largely low. Some of the uncertainties that hinder their endorsement are captured here, and options to refine them and to enhance their adoption are discussed.

Keywords Disease · Management · Mealybugs · Prevention · Removal · Rogueing · Uncertainties · Vectors · Virus · *Vitis*

Introduction

Grapevines host the most viruses among cultivated crop species (Martelli 2018). The occurrence of a multitude of viruses − 86 different species to date (Table 1) − is likely explained by (i) an extended coexistence with their *Vitis* spp. hosts, (ii) a very long history of *Vitis* domestication (Reynolds 2017), (iii) a sparsity of resistance sources in *Vitis* spp. (Oliver and Fuchs 2011), (iv) an extensive exchange of *Vitis* germplasm on a global scale (Martelli 2017), and (v) the advent of high throughput sequence technologies for virus identification (Saldarelli et al. 2017a). Several grapevine viruses are the causal agents of detrimental diseases, i.e., degeneration (grapevine fanleaf virus-GFLV, arabis mosaic virus-ArMV and viruses alike), red blotch (grapevine red blotch virus-GRBV), leaf mottling and deformation (grapevine Pinot gris virus-GPGV). Others are associated with major diseases such as vein clearing (grapevine vein clearing virus-GVCV) and Roditis leaf discoloration (grapevine Roditis leafroll discoloration-associated virus-GRLDaV) at a local scale or are associated with disease complexes such as leafroll, rugose wood and fleck that are widespread (Martelli 2017, 2018) (Table 1).

The management of grapevine virus diseases has prevention and suppression of the virus inoculum in the vineyard as main goals (Golino et al. 2017a, b; Maliogka et al. 2015). Preventing the introduction of viruses in newly established vineyard parcels is primarily achieved by carefully selecting planting material derived from virus-tested (negative) foundation vine stocks (Golino et al. 2017a). Reducing the virus inoculum in diseased vineyards is essentially achieved by rogueing and removal of entire parcels, eventually in combination with the control of vector populations, depending on the level of virus incidence and spread dynamics. Virus disease management solutions in the vineyard often require the integration of tailored tactics and are realized at the estate or regional scales.

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Table 1 Viruses identified in grapevine to date (updated from Martelli 2018)

Family[a]	Genus[a]	Species[a]	Genome	Particle shape[b]	Vector[c]	Disease[d]
Alphaflexiviridae	*Potexvirus*	*Potato virus X* (PVX)	(+)ssRNA	Filamentous	None	Unknown
Betaflexiviridae	*Fivirus*	*Grapevine Kizil Sapak virus* (GKSV)	(+)ssRNA	Filamentous	Unknown	Unknown
	Foveavirus	*Grapevine rupestris stem pitting-associated virus* (GRSPaV)	(+)ssRNA	Filamentous	Unknown	Rugose wood
		Grapevine virus T (GVT)				
	Trichovirus	*Grapevine berry inner necrosis virus* (GINV)	(+)ssRNA	Filamentous	Eriophyid mite	Berry inner necrosis
		Grapevine Pinot gris virus (GPGV)				Leaf mottling/deformation
	Vitivirus	*Grapevine virus A* (GVA)	(+)ssRNA	Filamentous	Mealybugs, soft scales	Rugose wood
		Grapevine virus B (GVB)				
		Grapevine virus D (GVD)				
		Grapevine virus E (GVE)				
		Grapevine virus F (GVF)				
		Grapevine virus G (GVG)				
		Grapevine virus H (GVH)				
		Grapevine virus I (GVI)				
		Grapevine virus J (GVJ)				
		Grapevine virus K (GVK)				
		Grapevine virus L (GVL)				
		Grapevine virus M (GVM)				
Bromoviridae	*Alfamovirus*	*Alfalfa mosaic virus* (AMV)	(+)ssRNA	Bacilliform	Aphids	Yellow mosaic
	Anulavirus	Related to *Amazon lily mild mottle virus* (ALiMMV)	(+)ssRNA	Isometric	None	Unknown
	Cucumovirus	*Cucumber mosaic virus* (CMV)	(+)ssRNA	Isometric	Aphids	Unknown
	Ilarvirus	*Grapevine angular mosaic virus* (GaMoV)	(+)ssRNA	Isometric	None	Angular mosaic
		Grapevine line pattern virus (GLPV)				
		Grapevine virus S (GVS)				Line pattern
Bunyaviridae	*Tospovirus*	*Tomato spotted wilt virus* (TSWV)	(−)ssRNA	Isometric	Thrips	Unknown
Caulimoviridae	*Badnavirus*	*Grapevine vein clearing virus* (GVCV)	dsDNA	Isometric	Aphids	Vein clearing
		Grapevine badnavirus 1 (GBV1)				Unknown
		Grapevine Roditis leaf discoloration-associated virus (GRLDaV)				Roditis discoloration
Closteroviridae	*Closterovirus*	*Grapevine leafroll-associated virus 2* (GLRaV2)	(+)ssRNA	Filamentous	Unknown	Leafroll/Incompatibility
	Ampelovirus	*Grapevine leafroll-associated virus 1* (GLRaV1)	(+)ssRNA	Filamentous	Mealybugs, soft scales	Leafroll
		Grapevine leafroll-associated virus 3 (GLRaV3)				
		Grapevine leafroll-associated virus 4 (GLRaV4)				
		Grapevine leafroll-associated virus 13 (GLRaV13)			Unknown	Leafroll
	Velarivirus	*Grapevine leafroll-associated virus 7* (GLRaV7)	(+)ssRNA	Filamentous	Unknown	Unknown
Endornaviridae	*Endornavirus*	*Grapevine endophyte endornavirus* (GEEV)	(+)ssRNA	None	None	Unknown
Geminiviridae	*Begomovirus*	*Grapevine begomovirus A* (GBVA)	ssDNA	Twinned	Whiteflies	Unknown
	Grablovirus	*Grapevine red blotch virus* (GRBV)	ssDNA	Twinned	Treehopper	Red blotch
		Wild Vitis latent virus 1 (WVV1)			Unknown	Unknown
	Unassigned	*Grapevine geminivirus A* (GGVA)	ssDNA	Twinned	Unknown	Unknown
		Temperate fruit-decay-associated virus (TFDaV)				
Luteoviridae	*Enamovirus*	*Grapevine enamovirus 1* (GEV1)	(+)ssRNA	Isometric	Aphids	Unknown
Partitiviridae	*Deltapartitivirus*	*Grapevine cryptic virus* (GCV)			None	Unknown
Phenuiviridae	*Rubodvirus*	*Grapevine Garan dmak virus* (GGDV)	(−)ssRNA	Isometric	Unknown	Unknown
		Grapevine Muscat rose virus (GMRV)				Unknown
Potyviridae	*Potyvirus*	*Bean common mosaic virus* (BCMV)	(+)ssRNA	Filamentous	Aphids	Unknown
		Potato virus Y (PVY)				
Reoviridae	*Unassigned*	*Grapevine Cabernet Sauvignon reovirus* (GCSV)	dsRNA	Isometric	Plant/Leafhoppers	Unknown
Secoviridae	*Cheravirus*	*Apple latent spherical virus* (ALSV)[e]	(+)ssRNA	Isometric	Unknown	Unknown
	Fabavirus	*Broad bean wilt virus* (BBMV)	(+)ssRNA	Isometric	Aphids	Unknown
		Grapevine fabavirus (GFabV)				
	Nepovirus	*Artichoke Italian latent virus* (AILV)	(+)ssRNA	Isometric	Unknown	Degeneration
		Arabis mosaic virus (ArMV)			Dagger nematode	
		Blueberry leaf mottle virus (BBLMV)			Unknown	
		Cherry leafroll virus (CLRV)				
		Grapevine Anatolian ringspot virus (GARSV)				
		Grapevine Bulgarian latent virus (GBLV)				
		Grapevine deformation virus (GDeV)				

Table 1 (continued)

Family[a]	Genus[a]	Species[a]	Genome	Particle shape[b]	Vector[c]	Disease[d]
		Grapevine chrome mosaic virus (GCMV)				
		Grapevine fanleaf virus (GFLV)			Dagger nematode	
		Grapevine Tunisian ringspot virus (GTRV)			Unknown	
		Peach rosette mosaic virus (PRSM)			Dagger nematodes	
		Raspberry ringspot virus (RpRSV)				
		Tobacco ringspot virus (TRSV)				
		Tomato ringspot virus (ToRSV)				
		Tomato black ring virus (TBRV)				
	Unassigned	*Strawberry latent ringspot virus* (SLRSV)			Dagger nematodes	
Tombusviridae	*Carmovirus*	*Carnation mottle virus* (CarMV)	(+)ssRNA	Isometric	None	Unknown
	Necrovirus	*Tobacco necrosis virus D* (TNV-D)	(+)ssRNA	Isometric	None	Unknown
	Tombusvirus	*Grapevine Algerian latent virus* (GALV)	(+)ssRNA	Isometric	None	Unknown
		Petunia asteroid mosaic virus (PAMV)				
Tymoviridae	*Marafivirus*	*Blackberry virus S* (BlVS)	(+)ssRNA	Isometric	Leafhoppers	Unknown
		Grapevine asteroid mosaic-associated virus (GAMaV)				Asteroid mosaic
		Grapevine asteroid mosaic-associated virus (GAMaV)				Fein feathering
		Grapevine Syrah virus 1 (GSyV1)				Unknown
	Maculavirus	*Grapevine fleck virus* (GFkV)	(+)ssRNA	Isometric	Unknown	Fleck
		Grapevine redglobe virus (GRGV)				Unknown
	Gratylivirus	*Grapevine-associated tymo-like virus* (GaTLV)	(+)ssRNA	Isometric	Unknown	Unknown
Virgaviridae	*Tobamovirus*	*Grapevine virga-like virus* (GVLV)	(+)ssRNA	Rod	None	Unknown
		Tobacco mosaic virus (TMV)				
		Tomato mosaic virus (ToMV)				
Unassigned	*Idaeovirus*	*Raspberry bushy dwarf virus* (RBDV)	(+)ssRNA	Isometric	None	Yellow line pattern
	Sobemovirus	*Sowbane mosaic virus* (SoMV)	(+)ssRNA	Isometric	None	Unknown
	Virtovirus	*Grapevine virus satellite* (GV-Sat)	(+)ssRNA	Isometric	Beetles	Unknown
	Unassigned	*Grapevine Ajinashika virus* (GAgV)	(+)ssRNA	Isometric	Unknown	Unknown
		Grapevine labile rod-shaped virus (GLRSV)	Unknown	Filamentous	Unknown	Unknown
		Grapevine stunt virus (GSV)		Isometric	Leafhopper	Unknown

[a] Some of the taxonomic affiliations and virus names are tentative, as ratifications by the International Committee on Taxonomy of Viruses are pending

[b] The shape of some virions is predicted by analogy with other viruses of the same genus or the same family rather than from actual electron micrograph observations

[c] Some of the vectors are deduced by analogy with vectors of other viruses of the same genus rather than from conclusive transmission assays

[d] Most virus disease symptoms cannot be attributed to a single virus species, as symptomatic vines are predominantly mixed infected in the vineyard, unless Koch's postulates have been fulfilled

[e] Apple latent spherical virus infects experimentally grapevine seedlings and tissue-cultured grapevines as a virus vector (Maeda et al. 2020). This virus was not identified in naturally infected vines

Management solutions of virus diseases are simple but their implementation in the vineyard is often suboptimal. Also, the adoption of management solutions is largely low at the global scale, in spite of their ecological and economical validations, as well as their documented successes for leafroll disease (Almeida et al. 2013; Bell et al. 2017, 2018; Pietersen et al. 2013, 2017). Several uncertainties explain a poor endorsement of management solutions in the vineyard. These need to be captured and addressed to describe weaknesses and recognize opportunities for improvement. Here, some of the uncertainties are reviewed and contingencies to refine virus disease management strategies in the vineyard and enhance their adoption by growers and vineyard managers are discussed.

A multitude of diverse viruses in grapevine

A total of 86 viruses have been isolated to date from grapevines worldwide (Table 1). The majority of grapevine viruses have only *Vitis* spp. as their natural host. About one third of them, particularly members of the plant virus families *Betaflexiviridae*, *Caulimoviridae*, *Closteroviridae*, *Geminiviridae* and *Secoviridae* are causing or are associated with economically damaging diseases such as leaf mottling and deformation, vein clearing, leafroll, red blotch and degeneration (Table 1). The genome of these detrimental viruses consists of single-stranded mono- (closterovirids and betaflexivirids) or bipartite RNA (secovirids) molecules, or single-stranded (geminivirids) or double-stranded DNA

(caulimovirids) molecules that are encapsidated in isometric, filamentous and (theoretically) twinned particles (Table 1). Their vectors are mealybugs (Hemiptera: Pseudococcidae), soft scale insects (Hemiptera: Coccidae) (Herrbach et al. 2017), eriophyid mites (Acari: Eriophyidae) (Saldarelli et al. 2017b), dagger nematodes (Nematoda: Longidoridae) (Andret-Link et al. 2017), a treehopper (Hemiptera: Membracidae) (Cieniewicz et al. 2017a) and an aphid (Hemiptera: Aphididae) (Qiu and Schoelz 2017; Petersen et al. 2019) (Table 1). Their distribution is wide with the exception of vein clearing and red blotch diseases, which are primarily restricted to the United States (Cieniewicz et al. 2020; Martelli 2017).

Another third of the viruses isolated from grapevines to date, particularly members of the plant virus families *Betaflexiviridae* (grapevine berry inner necrosis virus) and *Caulimoviridae* (grapevine Roditis leafroll discoloration-associated virus), are associated with detrimental diseases at a local scale (Table 1), while other members of the families *Betaflexiviridae* and *Tymoviridae* are widespread and associated with disease complexes, i.e., rugose wood and fleck (Table 1), that predominantly manifest when virus-susceptible rootstocks, i.e. *Vitis rupestris* and Kober 5BB (*V. berlandieri* x *V. riparia*), are used in the vineyard (Martelli 2017).

The remaining third of the grapevine viruses characterized to date have no marked detrimental impact on vine growth, fruit production or fruit quality. They belong to the plant virus families *Alphaflexiviridae*, *Bunyaviridae*, *Endornaviridae*, *Virgaviridae* or are unassigned to any plant virus family (Table 1).

Prevention is a cornerstone of management

Prevention is an essential component of virus disease management in grapevine. Preventive measures consist of the identification and production of virus-tested (negative) vines as a result of extensive indexing in combination with therapeutics methodologies for virus elimination, if appropriate (Golino et al. 2017a). Virus-tested vines are the backbone of sustainable viticulture. They are primarily maintained in foundation vineyards referred to as G1 blocks (Gergerich et al. 2015; Golino et al. 2017a). Only a limited number of vines (2-5) are usually kept for each clean accession (i.e., cultivar, clone, genotype, selection, etc.) in G1 foundation vineyards. Material from G1 blocks is then established in increase vineyards, referred to as G2 blocks, to bulk up the number of propagative units needed for the production of planting material to be sold to growers. Material from G2 blocks can be further propagated and established in G3 blocks, and material from G3 blocks can also be used for the establishment of G4 blocks. Vineyards with G2, G3 or G4 material are usually established and maintained by nurseries (Gergerich et al. 2015, Golino et al. 2017a). The production, establishment and maintenance of clean, virus-tested vines in G1 foundations and those derived from these vines that are in G2-G4 increase vineyards is laborious and costly. However, these virus-tested foundation vine stocks are essential for the production of clean, high-quality planting material and for the establishment of healthy vineyards in support of sustainable viticulture.

When using rootstock and scion material derived from virus-tested foundation vine stocks, the potential for planting virus-infected vines in the vineyard is low. In recent years, the production and establishment of virus-tested vines in G1 foundations and increase vineyards has reached an unprecedented level of cleanliness with regard to an extremely limited presence of economically damaging viruses, as recently documented in California where surveys of 24 commercial vineyards of varying age for eight different viruses documented substantially more viruses in old vineyards (1880-1995) than in vineyards recently planted with material derived from virus-tested stocks (1996-2014) (Arnold et al. 2019). These surveys are good testaments to the overall cleanliness of planting material recently derived from virus-tested foundation vine stocks. The fact that GRBV was found during these surveys in a few of the vineyards established in 2011-2014 is not too surprising based on the discovery of this virus in 2011, the availability of specific diagnostic assays in 2012, and the inclusion of the virus in the California certification program in 2016 (Arnold et al. 2019; Cieniewicz et al. 2020). Similarly, recent progress on the development of robust diagnostic methodologies (Al Rwahnih et al. 2015; Blouin et al. 2017; Rowhani et al. 2017; Saldarelli et al. 2017a) and sanitation techniques (Golino et al. 2017a) has been remarkable. These technologies have undoubtly facilitated the production of clean vines and transformed the quality of the planting material.

The benefits of using planting material derived from virus-tested foundation stocks in the vineyard are tremendous. These benefits are of economic, viticulture, wine making (fruit composition and wine chemistry), and environmental importance (Atallah et al. 2012; Fuller et al. 2019; Golino et al. 2017a; Ricketts et al. 2015, 2017).

Options to improve preventive measures

The health status of clean vines in G1 foundation and in increase vineyards can be compromised due to the influx of vectors carrying viruses. Maliogka et al. (2015) argued that "a challenge and target of future research is not so much the development of more refined and highly performing techniques for the recognition or the elimination of viruses but, rather, the design of dependable strategies for preventing a quick sanitary deterioration of vineyards planted with costly certified materials". These authors underscored the strategic

need for solutions to impede the introduction of viruses in G1 foundations and increase vineyard blocks, and to minimize their persistence. An elegant option to minimize exposure to viruliferous vectors is to establish and maintain foundation and increase vines in greenhouses or screenhouses (Golino et al. 2017b). This is a safe but very costly approach.

Monitoring virus infections in foundation and increase vineyard blocks often relies on visual observations alongside some minimal testing of randomly selected vines, or suspect vines that exhibit virus-like symptoms, even in areas where vector-mediated transmission of viruses is known to occur. The efficacy of these approaches is limited because (i) symptomatic, infected vines can serve as inoculum for secondary virus spread before their identification, (ii) virus infection in rootstocks is mostly latent, and (ii) statistically-supported sampling methodologies are usually not selected for the monitoring of the health status of vines. Consequently, actionable measures, i.e., the elimination and destruction of symptomatic, infected vines, are implemented late, often only after a virus is introduced and well established in a foundation or in an increase vineyard.

Ideally, virus-infected vines in foundation and increase vineyards should be detected as early as possible, preferentially at a pre-symptomatic stage, so that they can be eliminated immediately. Acting diligently to quickly identify and eliminate virus-infected vines is essential to avoid extended secondary spread. One solution is to test annually the health status of every vine in a G1 foundation vineyard for hemipteran-transmitted viruses such as those involved in vein clearing, leafroll, leaf mottling and deformation or red blotch diseases using laboratory diagnostic assays. The viruses targeted for such monitoring efforts should be dictated by local factors. For example, vines could be tested for grapevine leafroll-associated virus 3 (GLRaV-3) in areas where mealybug-mediated transmission of this virus is documented. In other areas, vines could be tested annually for GVCV where aphid-mediated transmission of this virus is known to occur, while, in other instances, it could be GRBV if treehopper transmission is reported or GPGV if eriophyid mite-mediated transmission occurs. An annual testing of vines of G1 foundation vineyards requires high throughput laboratory diagnostic capacity and adequate resources with regard to relevant equipment and trained personnel. To facilitate a high throughput testing, composite samples can be considered to lower the number of assays without affecting the ability to accurately identify virus-infected vines. Needless to mention, an accurate identification of virus-infected vines requires a sampling of appropriate vine tissues at the optimal time during the vegetative or dormant season. Any suboptimal sampling will result in false negative test results.

The health status of vines in increase vineyards should similarly be regularly monitored, especially if established in areas where vector-mediated transmission of detrimental viruses is reported. The intensity and frequency of sampling and testing of vines in increase vineyards should ideally be based on a zero tolerance for economically damaging viruses. Accepting any tolerance level inevitably means admitting the presence of virus-infected vines in increase vineyard blocks and, subsequently in the planting material, as well as their contribution to secondary virus spread. Preventing the presence of infected vines in increase vineyards is as critical as for vines in foundation vineyards. This is because a mother vine at a nursery is expected to produce an average of 250 buds (scion) and 135 cuttings (rootstocks) for grafting. Assuming a very conservative 60% graft-take, a single scion mother vine in an increase block can produce 150 grafted vines. If one is further conservatively assuming that only 50% of the buds collected from an infected scion mother vine actually contain the virus, a total of 75 virus-infected grafted vines can be produced annually from a single vine that is infected with a virus in an increase vineyard block. Similarly, a total of 41 virus-infected grafted vines can be produced annually from a single rootstock mother vine that is infected with a virus in an increase vineyard block. As a direct consequence of the presence of a virus in a single rootstock mother vine and in a single scion mother vine in an increase vineyard, 41 to 116 virus-infected grafted vines will be produced and transferred to the vineyard. Needless to say, the number of virus-infected vines for planting increases proportionally with the number of virus-infected scion and rootstock mother vines present in increase vineyard blocks. Once in the vineyard, virus-infected vines will potentially contribute to new epidemics.

In the United States, free-living *Vitis* and related *Ampelopsis cordata* vines in riparian areas near foundation and increase vineyards should be considered for removal. This is because they can potentially serve as virus reservoirs, including of vector-transmitted viruses such as GRBV, GVCV, GLRaV-3, grapevine virus A (GVA) and grapevine virus B (GVB) (Beach et al. 2017; Cieniewicz et al. 2018; Klaassen et al. 2011). Similarly, alternate hosts of GPGV in and around foundation vineyards should be eliminated to reduce the potential for spread (Cieniewicz et al. 2020).

A stringent agrochemical program should be considered in foundation and increase vineyard blocks to minimize the presence of vectors of economically damaging viruses. This is critical to reduce the likelihood of clean vines to become infected following a visit by viruliferous vectors. Also, vines in increase and foundation blocks could be treated with insect deterrents to discourage hemipteran vectors, including viruliferous specimens, from landing on clean vines. This should minimize the infection rate of clean vines and reduce outbreaks of vector-borne diseases. Nonetheless, a regular verification of the health status of vines in increase and foundation vineyards should be the prime priority over insect vector control to maintain the integrity of the health status of the material used for the production of vines for planting. To screen

foundation and increase vineyards for viruses, hyperspectral sensors and imaging techniques have the potential to facilitate surveys of large areas and accurately identify infected vines even at a pre-symptomatic infection stage (Bendel et al. 2020; Naidu et al. 2009; Mehrubeoglu et al. 2016; MacDonald et al. 2016). It will be interesting to see of these technologies will be deployed to detect viruses in foundation and increase vineyards. Additionally, canines have the olfactory ability to detect profiles of plant volatile organic compounds that are disease specific, as shown for plum pox virus, little cherry disease, citrus canker (Dininny 2019) and citrus greening (Gottwald et al. 2019). If canines were trained to detect virus-infected grapevines, they could be used to screen foundation and increase vineyards for early virus detection.

Certification programs regulate the production and distribution of clean vines that have viticultural characteristics of interest to the grape and wine communities and are derived from virus-tested foundation stocks. These programs are critical for the production and delivery of healthy and high-quality planting material to growers (Golino et al. 2017b; Maliogka et al. 2015). Successful certification programs are realistic and meaningful. Unfortunately, some programs can be disappointing because they are not enforced or are archaic; the later have usually not evolved since their inception several decades ago. Others are not satisfactory because they exclusively rely on visual inspections or do not consider the latest diagnostic technologies for the identification of virus-infected vines in foundation and increase vineyards. Suboptimal diagnostic methodologies can compromise the accuracy and specificity of virus detection. Similarly, many certification programs do not recognize the latest information on disease ecology, and thus, they poorly address situations of virus introductions in foundation and increase vineyards from aerially dispersing viruliferous vectors. Finally, some certification programs have low standards to satisfy harmonization efforts that often consider the lowest common biological denominator and trade values rather than the greatest common biological denominator and the global cleanliness of certified vines (Golino et al. 2017b). Based on recent progress in grapevine virus diagnostics and disease ecology, it would be beneficial if most, if not all, certification programs would be thoroughly evaluated and reimagined to embrace the latest advancements in these fields. This would have the merit to increase confidence in the cleanliness of the certified material.

Management solutions in the vineyard

In the vineyard, virus disease management relies on extensive scouting, rogueing or elimination of entire parcels and, if appropriate, applications of agrochemicals to control vector populations (Almeida et al. 2013; Maliogka et al. 2015; Pietersen et al. 2017). Replacements should be with clean planting material, including, if opportune, *Xiphinema index*-tolerant rootstocks in fanleaf diseased vineyards (Fuchs and Lemaire 2017) or *Planococcus ficus*-tolerant rootstocks (Naegele et al. 2020) in leafroll affected vineyards. A 4-5-year study on the spatiotemporal dynamics of leafroll disease in California vineyards recently confirmed a significant contribution of grape mealybug abundance and supply of GLRaV-3 to the frequency of newly diseased vines (Cooper et al. 2018). These results substantiated that leafroll disease management should target both the vector via population suppression approaches and the virus inoculum via the removal of diseased vines. These integrated solutions have been successfully adopted for the management of leafroll disease in South Africa and New Zealand (Bell et al. 2018; Pietersen et al. 2013, 2017).

Economic studies predicted the merit of rogueing in combination with insecticide applications to reduce mealybug populations when leafroll disease prevalence is low (between 5 and 10%), while a full vineyard replacement should be pursued if disease prevalence is higher, generally above 25%, although regional differences were clearly noted among the three studied grape-growing regions in California (Ricketts et al. 2015). Other studies reached similar conclusions in New York (Atallah et al. 2012), New Zealand (Nimmo-Bell 2006; Pietersen et al. 2017), South Africa (Pietersen et al. 2017) and the north coast of California (Fuller et al. 2019). These economically-attractive leafroll disease management recommendations should be considered as guidelines to strategically devise a customized actionable list of corrective measures at a parcel, estate or regional scale. This is because singularities among estates and grape-growing regions in terms of vineyard management practices and tolerance to leafroll disease need to be captured for the development of tailored solutions.

Given a predominant leafroll spread at a short spatial scale by crawling mealybugs and the aerial dispersal of viruliferous mealybugs from infected neighboring vineyard parcels, removal of individual infected vines, when disease incidence is low, delays the buildup of the virus in the vineyard (Arnold et al. 2017). Over time, if rogueing is not adopted, newly infected vines add to the source of inoculum, allowing mealybugs to transmit the virus to neighboring vines more readily. Since secondary inoculum drives the dynamics of leafroll epidemics, the virus can become difficult to manage if disease incidence is allowed to increase to the points where the inoculum is very high (Arnold et al. 2017). Therefore, an annual removal of infected vines suppresses the virus availability for secondary spread (Arnold et al. 2017; Bell et al. 2017, 2018; Pietersen et al. 2017).

For fanleaf degeneration, a careful removal of infected vines following their destruction via the application of a systemic herbicide and soil disinfection in combination with a fallow period should precede replanting efforts with vines grafted onto a rootstock tolerant to *X. index*, the dagger nematode vector of GFLV (Fuchs and Lemaire 2017).

For red blotch disease, recent epidemiological (Cieniewicz et al. 2017b, 2019a; Dalton et al. 2019) and economic studies (Ricketts et al. 2017) informed management strategies of this new threat to the grape industry (Cieniewicz et al. 2017a). These consist of rogueing and removal of entire vineyard parcels without the application of insecticides (Cieniewicz et al. 2019b, 2020). This is because populations of the threecornered alfalfa hopper (*Spissistilus festinus*) vector of GRBV are low in vineyards, predominantly visit vineyards during a short period during the growing season (Cieniewicz et al. 2017b, 2019a) and do not reproduce on grapevines (Preto et al. 2018). Rogueing symptomatic vines and selecting replants derived from virus-tested stocks are predicted to minimize economic losses if the incidence of red blotch disease is low to moderate (below 30%), while a full vineyard replacement should be pursued if disease incidence is higher, generally above 30% (Ricketts et al. 2017).

Options to improve management strategies in the vineyard

Virus disease management solutions are constantly refined for maximum efficacy. Great strides have been made in this area for leafroll disease management. For example, a long-lasting question for leafroll management is the removal of diseased vines with regard to rogueing. Is the elimination of individual symptomatic vines sufficient to reduce the virus inoculum in a leafroll diseased vineyard and limit mealybug-mediated virus spread? Or, should vines proximal to symptomatic ones also be considered for removal? The removal of symptomatic vines has worked well in South Africa and Zealand (Bell et al. 2017, 2018, Pietersen et al. 2017). Nonetheless, studies of profit-maximizing leafroll disease management strategies predicted that a spatial solution strategy is the optimal approach compared to a non-spatial strategy. In other words, rogueing symptomatic vines and one (Nimmo-Bell 2006) or two (Atallah et al. 2015) adjacent vines on each side is superior with regard to expected economic benefits compared to rogueing only symptomatic vines. Also, rogueing is recommended as early as possible rather than late to realize the full benefits of a healthy, productive vineyard and avoid damages in the future (Atallah et al. 2012). These predictions are based on epidemiological features of leafroll epidemics, indicating that a vine proximal to an infected, symptomatic one is highly likely to be visited by viruliferous mealybugs and probably to become infected prior to exhibiting disease symptoms if infected vines are aggregated. To this end, experimental vines inoculated by viruliferous mealybugs in a vineyard became symptomatic after one growing season following a 48-h inoculation access period, although one third of them 30% (20 of 60) were already infected by GLRaV-3 four months post-inoculation, as shown by reverse transcription quantitative polymerase chain reaction (Blaisdell et al. 2016). Therefore, eliminating asymptomatic vines that are adjacent to infected, symptomatic vines before they contribute to virus spread is critical to contain leafroll disease epidemics (Atallah et al. 2015).

A visual identification of virus-infected vines in the vineyard can be challenging for some diseases, e.g., leafroll and red blotch, particularly in those established with white-berried cultivars (Cieniewicz et al. 2017a; Pietersen et al. 2017). Robust diagnostic methodologies (Al Rwahnih et al. 2015, Blouin et al. 2017, Rowhani et al. 2017, Saldarelli et al. 2017a) are available for leafroll and red blotch viruses, as well as for the other viruses of grapevine recently identified (Debat et al. 2020), but most of them require sophisticated equipment in the laboratory and highly trained personnel. To facilitate the identification of infected vines in the vineyard, diagnostic assays applicable onsite would be desirable. Ideally, an in situ diagnostic assay should be cheap, fast, accurate, sensitive, specific, simple and easy to implement. Technologies such as lateral flow immunoassay, loop-mediated isothermal amplification (LAMP) and recombinase polymerase amplification (RPA) AmplifyRP® Acceler8® have potential for onsite applications. Immuno-strips (Byzova et al. 2018) and a LAMP assay (Walsh and Pietersen 2013) were developed for GLRaV-3. A LAMP assays is also available for GRBV (Romero Romero et al. 2019) and an RPA AmplifyRP® Acceler8® test was developed for GLRaV-3 (Li et al. 2019), GPGV (Li et al. 2019) and GRBV (Li et al. 2017). These assays have great potential in the vineyard to confirm the status of vines suspected of virus infection, particularly in white-berried cultivars, and assist the selection of the most appropriate disease management option. For example, onsite assays could help quickly circumscribe a virus disease in the vineyard, assist the determination of disease incidence and decide on the best strategy for rogueing by confirming the infectious status of symptomatic vines and proximal within-row vines. It is anticipated that onsite assays will be helpful to growers and vineyard managers after the completion of thorough validations in the vineyard. The identification and mapping of infected vines in the vineyard could also be aided by hyperspectral imaging, as elegantly documented for GLRaV-3 (MacDonald et al. 2016) or GLRaV-1 (Bendel et al. 2020) and explored for GRBV (Mehrubeoglu et al. 2016).

Alternate hosts of some viruses, i.e., GLRaV-3, GVA, GVB, GRBV and GVCV (Beach et al. 2017; Cieniewicz et al. 2018, 2019b, 2020; Klaassen et al. 2011), such as free-living *Vitis* and related *Ampelopsis cordata* vines in forested areas near commercial vineyards in the northern California and the heartland of the United States, as well as some shrubs and weeds in Europe (Cieniewicz et al. 2020), should be eliminated to limit the potential for spread.

Capturing management uncertainties

Virus disease management solutions are often difficult to implement in the vineyard or are poorly adopted by growers and

vineyard managers. This is more so if awareness of a virus disease problem among grower's communities is low and solutions are poorly communicated. For instance, a disconnect between the perception and the reality of how challenging a virus disease problem is can profoundly influence the likelihood of a successful virus disease management program. A crop is often harvested even in vineyards affected with the most detrimental viruses, although sub-standards fruits with regard to yield and composition are picked. Therefore, it is fairly common for a grower or a vineyard manager to take no action to mitigate the impacts of virus diseases. Furthermore, a distinct perception of a high-quality crop between a vineyard manager and a winemaker is not uncommon; this can create uncertainties on how to optimally act for the management of virus diseases in the vineyard.

The fact that chemicals are futile to combat viruses and no cure exists in vineyards adds other uncertainties on how to best manage virus diseases. Growers are used to apply agrochemicals to control most diseases in the vineyard and the triviality of this approach to manage virus diseases can be destabilizing. Uncertainties are also related to the impacts of viruses on fruit production and quality varying annually with the virome, the vineyard site, environmental conditions and cultural practices (Mannini and Digiaro 2017). This creates doubts on the urgency to act. In addition, uncertainties about the success of a management strategy can hinder the implementation of corrective actions. For example, applying insecticides against mealybugs is very often adopted by growers. Unfortunately, this action by itself is not sufficient to control leafroll disease. Similarly, rogueing without the application of insecticides can be suboptimal for leafroll disease management (Bell et al. 2018). A combination of removal of the virus inoculum and vector control is needed to mitigate the impacts of leafroll disease (Almeida et al. 2013; Atallah et al. 2012; Cooper et al. 2018; Fuller et al. 2019; Pietersen et al. 2017; Ricketts et al. 2015).

A perceived high cost of solutions can also prevent actions, in spite of several studies that convincingly support profit-maximizing leafroll disease management tactics (Atallah et al. 2012, 2015, 2017; Fuller et al. 2019; Nimmo-Bell 2006; Ricketts et al. 2015). Also, distinct appreciations of a virus impact can provide differential incentives to manage the disease at the local scale. This has implication for the management of leafroll disease. For example, the action of two vineyard managers producing grapes in two adjacent vineyard parcels can be spatially and dynamically consequential for the neighboring vineyard (Arnold et al. 2017; Atallah et al. 2017; Cooper et al. 2018). To this end, it is often admitted that a neighboring vineyard manager who does not take any action compromises proximal vineyards, thus limiting a desire to act at a local or at a regional scale. A cooperative management approach clearly pays off while non-cooperative approaches will not attain desirable outcomes in most cases. This means that the scope of the management goals can dictate the achievability of management solutions (Arnold et al. 2017, Atallah et al. 2017, Cooper et al. 2018).

Another factor that contributes to a low adoption of virus disease management solutions is a lack of trust in policies aimed at mitigating the presence of viruses in the propagation material. This is creating uncertainties that reduce the adoption rate of management tactics in the vineyard. For example, it is often perceived that certification programs are not satisfactorily addressing the needs of growers and that little has been done to reduce the extent of new virus outbreaks. Also, there is often no price differential between a vine derived from virus-tested stocks or from unscreened stocks. This may reduce the level of confidence in the cleanliness of certified vines from a grower's perspective. Curiously, nurseries often pay a fee per vine sold to the institution maintaining G1 foundation vineyards but this fee is rarely passed on to growers (Fuller et al. 2019). Applying a premium for clean, certified planting material may incentivize the adoption of material derived from virus-tested foundation vine stocks.

Addressing management uncertainties

Uncertainties are a critical aspect of virus disease management actions that need to be recognized, as they can be detrimental to the implementation of solutions in the vineyard. It is anticipated that addressing uncertainties will help to provide a stronger foundation for an enhanced adoption of solutions that are entrusted in ecology-driven and economically-attractive evidence.

To improve how uncertainties are captured, it is necessary to (i) relentlessly communicate on the biology and ecology of virus diseases to the community of growers and vineyard managers, as well as to policy makers, (ii) engage with agriculture economists to integrate an economically-appealing component into ecologically-sound disease management options to offer enticing solutions to growers and vineyard managers, (iii) disseminate recommendations on disease management options that resonate with growers and vineyard managers, (iv) be genuinely interested in helping growers and vineyard managers to gain their trust, (v) continuously dialogue with growers and vineyard managers to set realistic and meaningful management goals after clearly circumscribing the disease(s) and understanding its/their cause in the vineyard, (vi) devise tailored scenario-based disease management tactics at the estate or regional scale, (vii) establish lasting collaborative interactions with growers and vineyard managers to continuously encourage and guide their disease management efforts, (viii) learn the lessons from past failures or not so-rewarding efforts to continuously refine disease management solutions, (ix) work closely with policy makers and regulators to set meaningful and realistic certification programs that take into account the latest

advancements in disease ecology and virus diagnostics, and (x) be committed to support the sustainability of the grape and wine industry.

This sequence of synergistic endeavors is critical to improve the delivery of information that resonates loudly with growers and vineyard managers for enhancing the adoption of research-based virus disease management solutions. Similar endeavors are necessary with policy makers to develop sound regulations that are based on our current knowledge of disease ecology and recent virus diagnostic technologies. Finally, establishing and cultivating a long-lasting dialogue and cooperative relationships between researchers, extension educators, growers, vineyard managers, vintners, nurseries, marketing personnel, policy makers and regulators are paramount not only to remain impactful but also to ameliorate the level of confidence in our collective ability to accompany the production and distribution of clean vines derived from virus-tested foundation stocks for enhancing the efficacy of preventive strategies and fostering a broader adoption of virus disease management solutions in the vineyard.

Conclusions

About two thirds of the 86 viruses isolated from grapevines to date are causing or are associated with economically damaging diseases. Prophylactic measures and the production of clean vines derived from virus-tested foundation vine stocks are the backbone of sustainable viticulture. The health status of clean vines maintained in the vineyard can be compromised as a result of vector-mediated virus transmission. Based on recurrent or recent outbreaks, a more diligent monitoring of the health status of vines in foundation and increase vineyards is needed. Alternatively, foundation and increase vines could be established and maintained in greenhouses or screenhouses to minimize exposure to mobile viruliferous vectors. In the vineyard, rogueing and removal of entire parcels, in combination with the application of agrochemicals, if justified, and vine replacements with clean planting material, including vector tolerant rootstocks, if opportune, are critical to reduce the virus inoculum, lower vector populations and limit secondary virus spread. These solutions are simple but their adoption is largely very low. More coordinated communication efforts and engagement with growers and vineyard managers are needed to foster the adoption of these solutions. Similar efforts are required with policy makers to develop meaningful and realistic regulations for enhanced certification programs that are rooted on science-driven evidence. Such endeavors are essential to ameliorate the production and distribution of clean vines derived from virus-tested foundation stocks through improved preventive strategies and more widely-adopted virus disease management solutions in the vineyard. These actions should be part of a strategic process to address the raising demand for new management solutions of grapevine viruses.

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