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GRAPEVINE VIRUS DISEASES: ECONOMIC IMPACT AND CURRENT ADVANCES IN VIRAL PROSPECTION AND MANAGEMENT[1]

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ABSTRACT-Grapevine (*Vitis* spp.) is a major vegetative propagated fruit crop with high socioeconomic importance worldwide. It is susceptible to several graft-transmitted agents that cause several diseases and substantial crop losses, reducing fruit quality and plant vigor, and shorten the longevity of vines. The vegetative propagation and frequent exchanges of propagative material among countries contribute to spread these pathogens, favoring the emergence of complex diseases. Its perennial life cycle further accelerates the mixing and introduction of several viral agents into a single plant. Currently, approximately 65 viruses belonging to different families have been reported infecting grapevines, but not all cause economically relevant diseases. The grapevine leafroll, rugose wood complex, leaf degeneration and fleck diseases are the four main disorders having worldwide economic importance. In addition, new viral species and strains have been identified and associated with economically important constraints to grape production. In Brazilian vineyards, eighteen viruses, three viroids and two virus-like diseases had already their occurrence reported and were molecularly characterized. Here, we review the current knowledge of these viruses, report advances in their diagnosis and prospection of new species, and give indications about the management of the associated grapevine diseases.
Index terms: Vegetative propagation, plant viruses, crop losses, berry quality, next-generation sequencing.

VIROSES EM VIDEIRAS: IMPACTO ECONÔMICO E RECENTES AVANÇOS NA PROSPECÇÃO DE VÍRUS E MANEJO DAS DOENÇAS DE ORIGEM VIRAL

RESUMO-A videira (*Vitis* spp.) é propagada vegetativamente e considerada uma das principais culturas frutíferas por sua importância socioeconômica mundial. Ela é suscetível a vários agentes transmitidos por meio da enxertia, os quais causam diversas doenças e significativas perdas na produtividade e produção, redução na qualidade dos frutos, no vigor da planta e na longevidade dos vinhedos. A propagação vegetativa e o frequente intercâmbio de material propagativo entre países contribuem para a disseminação destes patógenos, favorecendo a emergência de doenças complexas. Seu ciclo de vida perene acelera ainda mais a mistura e a introdução de vários agentes virais em uma mesma planta. Atualmente, aproximadamente 65 vírus pertencentes a diferentes famílias foram reportados infectando videiras, embora nem todos causem doenças economicamente relevantes. As viroses do enrolamento da folha, complexo do lenho rugoso, degenerescência e mancha-das-nervuras da videira são as quatro principais desordens que têm importância econômica mundial. Além disso, novas espécies e estirpes virais foram identificadas e associadas a limitações economicamente importantes para a produção de uvas. Em vinhedos brasileiros, dezoito espécies virais, três viroides e duas doenças semelhantes a viroses já tiveram sua ocorrência reportada e foram molecularmente caracterizados. Aqui, nós revisamos o conhecimento atual dessas viroses, os recentes avanços na diagnose e prospecção viral, e fornecemos recomentações sobre o manejo das viroses da videira.
Termos para indexação: Propagação vegetativa, vírus de plantas, redução da produtividade e produção, qualidade das bagas, sequenciamento de nova geração.

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INTRODUCTION

Grapevine (*Vitis* spp.) is a major crop having a worldwide high socioeconomic importance (CAMARGO et al., 2011; RUIZ, 2011). It is susceptible to several graft-transmitted agents that cause or are associated with several diseases, whose etiology is yet unknown (MALIOGKA et al., 2015a; MARTELLI, 2014). Vegetative propagation and frequent exchanges of propagative material have contributed to worldwide spread of these pathogens, favoring the emergence of complex diseases (AL RWAHNIH et al., 2009; BASSO et al., 2014). Moreover, its perennial life cycle accelerated the mixing and introduction of several viral agents into a single plant (BARBA et al., 2015; MARTELLI, 2014). Grapevine viral diseases cause substantial crop losses, reduce plant vigor and shorten the longevity of vines. In addition, they also affect technological characteristics due to a delayed ripening and reduced quality of berries, with impact on sugar content, pigments and increased acidity of wines (BASSO et al., 2010c; BARBA et al., 2015; NASCIMENTO et al., 2015).

Currently, approximately 65 viruses, eight viroids and four satellite RNAs belonging to different families have been reported infecting grapevines (CHIUMENTI et al., 2016; FIORE, 2015; MALIOGKA et al., 2015a; MARTELLI, 2014) (Table 1). Grapevine leafroll, rugose wood complex, leaf degeneration and fleck disease are the four main disorders having a worldwide economic importance (ANDRET-LINK et al., 2004; MARTELLI, 2014; NAIDU et al., 2015). Grapevine viruses associated with these diseases have a RNA genome. Recently, DNA viral agents have been identified, such as a geminivirus associated with Red blotch disease in the USA (AL RWAHNIH et al., 2013b; KRENZ et al., 2012 and 2014; POOJARI et al., 2013), two badnaviruses associated with Grapevine vein-clearing and vine decline syndrome in the USA (ZHANG et al., 2011) and with Roditis leaf discoloration disease in Greece (MALIOGKA et al., 2015b), and a unclassified virus associated with fruit tree decline syndrome in the Brazilian orchards and vineyards (BASSO et al., 2015).

Disease expression may be influenced by environmental factors, grapevine cultivar, rootstock, viral isolate or strain, intrinsic agronomic conditions or association with others pathogens or viruses (MALIOGKA et al., 2015a). All these pathogens are disseminated across long distances by vegetative propagation (MARTELLI, 2014) whereas local plant-to-plant transmission is operated by insect, mite or nematode vectors (MALIOGKA et al., 2015a; MARTELLI, 2014) (Table 1).

The grapevine viruses control, as well as for other plant species, is inevitably based on determining the sanitary status of the vines. Therefore besides the experience in recognizing the symptoms caused by these pathogens, the availability of efficient detection techniques is important. Recent advances in molecular biology tools to study the viral population present in vineyards, allowed the efficient detection, identification and prospection of known or new viral species and strains (AL RWAHNIH et al., 2015; BURGER; MAREE, 2015; ROOSSINCK et al., 2015). Using next-generation sequencing technologies (NGS) (AL RWAHNIH et al., 2015) and rolling-circle amplification (RCA) strategies (INOUE-NAGATA et al., 2004) have enhanced the diagnosis tools and knowledge of grapevine virome (AL RWAHNIH et al., 2013b; BASSO et al., 2015; GIAMPETRUZZI et al., 2012; MALIOGKA et al., 2015b). In Brazilian vineyards, eighteen viruses, three viroids, two virus-like diseases and some phytoplasmas have been already reported and were molecularly characterized (BASSO et al., 2014) (Table 2 and 3).

This research presents the current state of knowledge of these economically important viruses in grape-growing countries, including Brazil, and report advances in their diagnosis and prospection, and give indications about the management of the associated diseases.

DAMAGES AND ECONOMIC IMPACT OF GRAPEVINE V IRUS DISEASES

Viruses and subviral agents are active only after being introduced into living cell, in which they replicate as parasites using the biological systems of the host cell and changing several physiological functions (FIORE, 2015). Viral disease effects in grapevines can manifest in more specific or more comprehensive forms, with variations that depend on the viral species or strains, grapevine cultivar and agronomic or climatic conditions. Infected plants exhibit changes in genes expression profile, carbohydrate metabolism and hormonal balances, decrease in photosynthetic potential, increase in respiration rate, interference in electron transport activity of photosystem I and II, reduction of the chlorophyll levels and soluble sugar accumulation in the leaves and deficiency in translocation of these sugars to sink tissues or grape berries (BASSO et al., 2010c; NAIDU et al., 2015).

In addition, there is up or down regulation of several genes involved in critical metabolic pathways, such as biosynthesis of primary or secondary metabolites, signaling, proteins associated with senescence (proteases, lipases, proteins involved in nutrient remobilization, transcription factors, proteins related to translation and antioxidant enzymes), defense-related genes to biotic or abiotic stress, and vegetative development of the host plants (ESPINOZA et al., 2007; VEGA et al., 2011). These stresses have effects in berry quality because of irregular ripening and affect plant growth resulting in a delay of sprouting, reduced tolerance to stresses and even death of the chronically infected plants (CRETAZZO et al., 2010 and 2013; GIRIBALDI et al., 2011; NASCIMENTO et al., 2015; VEGA et al., 2011). Grapes harvested from infected grapevines show reduced total soluble solid content (from 3 to 5 ºBrix), color intensity of red-berried cultivars of up to 35%, total polyphenol content of up to 38%, biosynthesis of tannins, flavonoids, anthocyanins, polyamines, aromatic compounds and other metabolites, and increase in titratable acidity of the must (ALABI et al., 2016; BASSO et al., 2010c; GUTHA et al., 2010; NAIDU et al., 2015). A recent study in the USA estimated that the economic impact of grapevine leafroll disease on the profit of grape businesses range from $25,000 to $40,000 per hectare for vineyards with a 25-year lifespan (ATALLAH et al., 2012).

MAJOR GRAPEVINE VIRAL DISEASES

Grapevine leafroll disease (GLRD): GLRD is the most economically damaging and widespread viral disease of grapevine throughout the world (ALABI et al., 2016; ALMEIDA et al., 2013; ATALLAH et al., 2012; NAIDU et al., 2014 and 2015). It can cause up to 40% yield losses (NAIDU et al., 2014). Several viral species designated *Grapevine leafroll-associated viruses* belonging to the family *Closteroviridae* (genus *Ampelovirus*, *Closterovirus* and *Velarivirus*) are related to GLRD, which can occur alone or as viral complex (MAREE et al., 2013; MARTELLI et al., 2012). The GLRaV-2 and -3 are the most prevalent and widely spread (MAREE et al., 2013; MARTELLI, 2014). The first symptoms in adult plants appear on mature leaves, always from the base of the canes, progressively moving upward to younger leaves, which is more pronounced at the end of the growing season, while young sproutings of grafted-vine cuttings are commonly asymptomatic (NAIDU et al., 2014; TSAI et al., 2012). The *V. vinifera* exhibit conspicuous symptoms, while *V. labrusca*, hybrids and rootstocks are often asymptomatic or the symptoms may be mild (BASSO et al., 2014). Typical symptoms are leaf reddening (in red-berried cultivars) or yellowing (in white-berried cultivars) with coriaceous texture while veins remain green and leaf edges roll downward (GLRaV-1 to -3). Some GLRaV-2 strains are cause of graft incompatibility (NAIDU et al., 2014) (Figure 1A and B). Asymptomatic leaves or milder symptoms can also be observed (GLRaV-4 and -7) (MALIOGKA et al., 2015a). Several soft scale and mealybug species are efficient vectors of the ampeloviruses in a semi-persistent transmission manner (Table 3) (LE MAGUET et al., 2012; TSAI et al., 2010 and 2012). However, no vector has been identified for GLRaV-2 and -7.

Grapevine rugose wood disease (GRWD): GRWD is a complex disease of grapevines in several growing regions (MALIOGKA et al., 2015a; MARTELLI, 2014). Four distinct syndromes are GRWD-associated: rupestris stem pitting, kober stem grooving, LN33 stem grooving and corky bark, which are often latent or mild symptoms in ungrafted vines and strongly evident in grapevine-grafted *V. vinifera* (MARTELLI, 2014). Associated agents are *Grapevine rupestris stem pitting-associated virus* (GRSPaV; genus *Foveavirus*) and *Grapevine viruses A*, *B*, and *D* (genus *Vitivirus*), all belonging to the *Betaflexiviridae* family (KING et al., 2012; MARTELLI et al., 2007). Typical symptoms in *V. vinifera* are characterized by alterations of the plant woody cylinder consisting in pitting and grooving of the region underneath the bark, which affect water and nutrient flow, cause reddening of the entire leaf blade, induce formation of corked bark in the internode region, provoke graft incompatibility, delayed budding, grapevine decline and eventually, plant death (MALIOGKA et al., 2015a; ROSA et al., 2011). In contrast, in *V. labrusca* a swelling of internodes in the branches of the year and tissue longitudinal splitting are observed (Figure 1C) (NICKEL et al., 2002). Stem pitting is observed in susceptible rootstocks such as Paulsen 1103 (*V. berlandieri* x *V. rupestris*) (Figure 1D) (MALIOGKA et al., 2015a; ROSA et al., 2011). GRWD-associated viruses are semi-persistently vectored by several mealybugs and soft scale insects (Table 3), while GRSPaV has no known insect vector and is not mechanically transmitted to herbaceous hosts (KING et al., 2012; LE MAGUET et al., 2012; MARTELLI, 2014). GLRD and GRWD are the two most economically important disease complexes in

Brazilian vineyards (BASSO et al., 2014).

Grapevine fanleaf degeneration disease (GFDD): GFDD is considered the most important grapevine disease in Europe and North American vineyards, which occurs in almost all grapevine cultivated regions (ANDRET-LINK et al., 2004; MALIOGKA et al., 2015a). Its main etiological agent is *Grapevine fanleaf virus* (genus *Nepovirus*) belonging to the *Secoviridae* family (MARTELLI, 2014). The GFDD is endemic to areas where its soil-borne nematode vector is present (VILLATE et al., 2008). Typical symptoms are leaf distortion, yellow mosaic close to primary veins, bright yellow vein banding on leaves, widely open petiolar sinuses, double nodes, short and malformed internodes (Figure 1E). In general, foliar symptoms appear at the beginning of the growing season. In Brazilian vineyards, GFLV has been reported, but apparently GFDD is not economically important (FAJARDO et al., 2000; RADAELLI et al., 2009). Probably the occurrence of specific nematode vectors is limited or grapevine cultivated soils do not support the survival of these vectors in Brazilian conditions. GFLV is semi-persistently vectored by both juvenile stages and adults of the ectoparasitic nematodes *Xiphinema index* and *X. italiae* (DEMANGEAT et al., 2010; COHN et al., 1970).

Grapevine fleck disease (GFkD): GFkD is reported from all viticultural countries in the world (MARTELLI, 2014). The associated virus is *Grapevine fleck virus* (GFkV) belonging to the *Tymoviridae* family, which is a non-mechanically transmissible virus associated with fleck symptoms (SABANADZOVIC et al., 2000 and 2001). Several GFkV-infected *V. vinifera* and rootstock cultivars are symptomless. GFkV causes latent infections in *V. vinifera* cultivars and induces typical foliar symptoms of vein clearing, leaf deformation and reduction of the vegetative growth in the sensitive indicator *V. rupestris* St. George (FAJARDO et al., 2012; MARTELLI, 2014) (Figure 1F). GFkV has no known insect vector. In Brazilian vineyards, GFkD has been reported, but its importance and damage were not specifically evaluated (BASSO et al., 2014; FAJARDO et al., 2012).

New emerging diseases of grapevine

Decline of Syrah grapevines: first observed in France (RENAULT-SPILMONT et al., 2004), it was subsequently reported in California vineyards (BATTANY et al., 2004), and has been associated with several viral species. Typical disease symptoms appear in older grapevines, which include leaf reddening and scorching, swelling of the graft union, superficial cracking and pitting of the woody tissue and stem necrosis (AL RWAHNIH et al., 2009). A virus, *Grapevine Syrah virus-1*, was discovered in symptomatic grapevines in California (USA) (AL RWAHNIH et al., 2009) that is widely spread worldwide (ENGEL et al., 2010; FAJARDO et al., 2015c; GLASA et al., 2015) but its association with the disease was not clearly demonstrated. Its presence in leafhoppers (vector for marafiviruses) collected from diseased vines has been reported (AL RWAHNIH et al., 2009).

Red blotch disease: first reported in California (USA) in 2008 (CALVI, 2011). In red-berried grapevine cultivars, foliar symptoms consist of red blotches of the basal leaves early in the season that can expand and coalesce across most of the leaf blade later in the season and extend to middle leaves of the shoots. In contrast, in white-berried cultivars symptoms are less conspicuous and generally involve irregular chlorotic areas that may become necrotic late in the season (SUDARSHANA et al., 2015). Diseased vines show reduced total soluble solids, fruit quality and a delayed ripening. The causal agent is the *Grapevine red blotch-associated virus* (GRBaV) which was recently shown to induce symptoms when inoculated in grapevine as cloned DNA (AL RWAHNIH et al., 2013b; FUCHS et al., 2015; POOJARI et al., 2013). GRBaV was confirmed infecting free-living vines (*Vitis* spp.), two of which were *V. californica* x *V. vinifera* hybrids, in a proximal field of cultivated grapevines (PERRY et al., 2016). The leafhopper *Erythroneura zic-zac* Walsh (POOJARI et al., 2013) was shown to transmit GRBaV but its role as vector is uncertain.

Vein-clearing and vine decline syndrome: emerged in 2004, from a commercial vineyard in Missouri (USA) (QIU et al., 2007). *Grapevine vein clearing virus* (GVCV) was found associated with vein-clearing symptom, shortening of the internodes, crinkled leaves, misshapen and smaller grape berries, with irregular shape and abnormal texture (GUO et al., 2014; ZHANG et al., 2011). GVCV has no known insect vector and its economic importance is not clearly defined. However it should be noted that some badnaviruses are transmitted by pseudococcid mealybugs (MARTELLI; SALDARELLI, 2015).

Chlorotic mottling and leaf deformation: reported in grapevine cv. *Pinot gris* in Trentino Alto Adige vineyards (Italy) since 2003 (GIAMPETRUZZI

et al., 2012), to which a new RNA virus, *Grapevine Pinot gris virus* (GPGV), was found associated. The virus has been reported infecting several varieties in many European Countries (BEUVE et al., 2015; GAZEL et al., 2016; GLASA et al., 2014; MARTELLI, 2014; SALDARELLI et al., 2015) and recently in Californian grapevines, USA (AL RWAHNIH et al., 2009; RIEGER, 2015) and China (FAN et al., 2016). Its association with the disease is not clearly established due to the existence of different viral strains and diverse cultivars susceptibility (SALDARELLI et al., 2015). However, the associated disease has an important economic impact since it affects plant vigor and reduces the yield. The eriophyid mite *Colomerus vitis* is a vector of GPGV (MALAGNINI et al., 2016) and the herbaceous plants *Silene latifolia* subsp. *alba* (Mill.) (bladder campion) and *Chenopodium album* L. (white goosefoot) can be considered as a reservoir of the GPGV (GUALANDRI et al., 2016).

Roditis leaf discoloration disease: first reported in Greek vineyards in the 1980s (RUMBOS; AVGELIS, 1989). *Grapevine roditis leaf discoloration-associated virus* (GRLDaV) was recently found associated with typical symptoms of yellow and/or reddish discolorations and deformations of the young leaves, while grape berries are reduced in number and size, and have lower sugar content (MALIOGKA et al., 2015b). Recently the virus was also discovered in symptomless vines in Apulia, Italy (GIAMPETRUZZI et al., 2015). Since natural disease spreading was observed and considering that the disease agent has been identified as a badnavirus, it is plausible to hypothesize that a vector, possibly a pseudococcid mealybug, be responsible for transmission (MARTELLI; SALDARELLI, 2015).

Fruit tree decline syndrome: a complex disease that could be caused by several pathogens in orchards and vineyards. Recently, a new viral agent, Temperate fruit decay-associated virus (TFDaV), has been identified in Brazil infecting apple and pear trees and grapevine and probably it could be associated with fruit tree decay symptoms (BASSO et al., 2015). In addition, different viruses (hitherto considered absent in Brazil), viroids and phytoplasmas [belonging to ribosomal groups 16SrI (subgroup B) and 16SrIII (subgroup J or F)], were recently reported in Brazilian vineyards and their spread and economic importance are being investigated (CATARINO et al., 2015; EIRAS et al., 2006; FAJARDO et al., 2015a, 2015b; 2015c; ROHR DOS SANTOS et al., 2015; NERONI, 2009) (Table 2).

CURRENT ADVANCES IN DIAGNOSIS METHODS

The application of accurate and reliable diagnosis methods has fundamental importance in programs that are intended to produce and maintain virus-free propagating material, and are crucially important to the success of any preventive and control strategies of grapevine viral diseases (MALIOGKA et al., 2015a; ROOSSINCK et al., 2015). Virus diagnosis has evolved over the years, moving from the monitoring of grapevine sanitary status, biological indexing, transmission electron microscopy (TEM), serological ELISA-based methods, probe-based nucleic acid hybridization, PCR-based molecular methods, to high-throughput sequencing technology (AL RWAHNIH et al., 2015; BURGER; MAREE, 2015; MALIOGKA et al., 2015a).

All these methods present important limitations and several advantages (BASSO et al., 2014). The biological indexing is time-consuming, limited for inconspicuous symptoms and latent infections, while TEM and micro- or macroarrays are low efficient or onerous (ABDULLAHI et al., 2011; MALIOGKA et al., 2015a; TERLIZZI et al., 2010; THOMPSON et al., 2012). ELISA- or PCR-based methods are limited to viruses for which antibodies or virus-specific nucleotide sequences are available, while being are more rapid and efficient (BASSO et al., 2010b; FAJARDO et al., 2007a; MALIOGKA et al., 2015a). Conventional RT-PCR or real-time RT-PCR and its variations are currently the most used methods in routine assays. Immunocapture RT-PCR allows greater sensitivity and specificity, while RT-qPCR allows single or multiplex viral detection, viral load quantification, differentiation of viral variants with high sensitivity, specificity and reproducibility (AL RWAHNIH et al., 2012; BESTER et al., 2012; DUBIELA et al., 2013; KUMAR et al., 2015; LÓPEZ-FABUEL et al., 2013; OSMAN et al., 2013). RCA method also has been successfully used in grapevine virus amplification and detection (BASSO et al., 2015; KRENZ et al., 2012). Specific protocols for nucleic acids isolation and purification from grapevine tissues have been strongly recommended to improve sensitivity (AKKURT, 2012; PICCOLO et al., 2012; XIAO et al., 2015). In addition, the plant development stage and specific tissues in which the virus reaches higher concentration should be observed to perform accurate and sensitive diagnostic tests (BASSO et al., 2010a; BEUVE et al., 2007).

Finally, NGS technologies combined with advanced bioinformatics tools has currently revolutionized the research involving grapevine

viruses (BARBA et al., 2014; BURGER; MAREE, 2015; ROOSSINCK et al., 2015). Several metagenomics studies were developed aiming to know the virome and causal agents of economically important grapevine diseases (AL RWAHNIH et al., 2009, 2013b and 2015; COETZEE et al., 2010; FAJARDO et al., 2015c; GIAMPETRUZZI et al., 2012; JO et al., 2015; POOJARI et al., 2013; ZHANG et al., 2011). In addition, several new viral species or strains of known viruses, mycoviruses, viroids and phytoplasmas were identified using NGS of total RNAs, siRNAs or dsRNAs isolated from specific tissues. However, the main current limitation of NGS-based approaches is high cost per sample sequenced. It is believed that in the near future costs may become more accessible. In contrast, NGS is a powerful technology that allows detection and discovery of viruses without any prior knowledge of their genome (BURGER; MAREE, 2015; ROOSSINCK et al., 2015).

ADVANCES IN MANAGEMENT STRATEGIES

The good health status of propagative material (cuttings, grafts, buds, rooted cuttings and grafted plants) is the main prophylactic measure to mitigate impact of virus diseases (OLIVER; FUCHS, 2011). The production and use of certified virus-tested propagative material reduce the inoculum potential, mainly in areas where vectors are present (MARTELLI, 2014). The establishment of vineyards in vector-free (e.g. nematodes) areas reduces local and long-distance dispersal of viruses (LAIMER et al., 2009; VILLATE et al., 2008). Measures such as rouging of symptomatic grapevines and possibly adjacent plants (and removing any remaining roots), chemical or biological control or management of insect- or nematode-vector, and cross-protection and conventional or transgenic grapevines tolerant or resistant to viruses or nematode-vector (ALMEIDA et al., 2013; ATALLAH et al., 2012; BELL et al., 2009; FUCHS et al., 2007; GAMBINO et al., 2010; KOMAR et al., 2008; OLIVER; FUCHS, 2011) are possible strategies for viral disease management. The nematode chemical control is often inefficient, environmentally improper and harmful to humans, while transgenic plants may represent a possible choice (LAIMER et al., 2009; MALIOGKA et al., 2015a).

siRNA-mediated engineered resistance or expression of artificial microRNAs (amiRNA) has been a powerful tool, but is actually limited to experimental cultivars or model plant (LAIMER et al., 2009; OLIVER; FUCHS, 2011; ROUMI et al., 2012). Sources of genetic resistance to grapevine viruses are not available. In contrast, a major genetic resistance locus to *X. index* was recently reported from grapevine (HWANG et al., 2010; XU et al., 2008).

The main sanitation techniques to eliminate grapevine viruses are thermotherapy *in vivo* or *in vitro* (KRIZAN et al., 2009; PANATTONI; TRIOLO, 2010), chemotherapy (LUVISI et al., 2011; SKIADA et al., 2013), meristem and shoot tip culture (MALIOGKA et al., 2009), somatic embryogenesis (BORROTO-FERNANDEZ et al., 2009; GAMBINO et al., 2011), electrotherapy and cryotherapy (BAYATI et al., 2011; WANG et al., 2008). However, the main limitation of the electro- and cryotherapy is the low efficiency and possible induction of host genetic changes (BARANEK et al., 2009). A higher efficiency in obtain virus-free grapevines was achieved by thermo- or chemotherapy associated with meristem and shoot tip culture.

TABLE 1- Viruses, viroids and satellite RNAs currently reported infecting grapevines (*Vitis* spp.) worldwide and its insect or nematode vectors.

Family	Genus	Viral species	Vector
Alphaflexiviridae	*Potexvirus*	*Potato virus X* (PVX)	Unknown
Betaflexiviridae	*Foveavirus*	*Grapevine rupestris stem pitting-associated virus* (GRSPaV) [+]	Unknown
	Trichovirus	*Grapevine berry inner necrosis virus* (GINV)	Mites
		Grapevine Pinot gris virus (GPGV)	Mites
	Vitivirus	*Grapevine virus A* (GVA) [+]	Mealybugs and soft scales
		Grapevine virus B (GVB) [+]	Mealybugs
		Grapevine virus D (GVD) [+]	Unknown
		Grapevine virus E (GVE)	Mealybugs
		Grapevine virus F (GVF)	Unknown
Bromoviridae	*Alfamovirus*	*Alfalfa mosaic virus* (AMV)	Aphids
	Cucumovirus	*Cucumber mosaic virus* (CMV)	Aphids
	Ilarvirus	Grapevine line pattern virus (GLPV)	Unknown
		Grapevine angular mosaic virus (GAMoV)	Unknown
Bunyaviridae	*Tospovirus*	*Tomato spotted wilt virus* (TSWV)	Thrips
Closteroviridae	*Closterovirus*	*Grapevine leafroll-associated virus 2* (GLRaV-2) [+]	Unknown
	Ampelovirus (Subgroup I)	*Grapevine leafroll-associated virus 1* (GLRaV-1) [+]	Mealybugs and soft scales
		Grapevine leafroll-associated virus 3 (GLRaV-3) [+]	Mealybugs and soft scales
	Ampelovirus (Subgroup II)	*Grapevine leafroll-associated virus 4* (GLRaV-4) [+] (strain 5^+, 6^+=De, 9, Car, Pr)	Mealybugs and soft scales
	Velarivirus	*Grapevine leafroll-associated virus 7* (GLRaV-7)	Unknown
Caulimoviridae	*Badnavirus*	*Grapevine vein clearing virus* (GVCV) [+]	Unknown
		Grapevine roditis leaf discoloration-associated virus (GRLDaV)	Unknown
Geminiviridae	und	Grapevine red blotch-associated virus (GRBaV) synonym: Grapevine cabernet franc-associated virus (GCFaV) and Grapevine redleaf-associated virus (GRLaV)	Leafhopper

continuation...

TABLE 1 - Viruses, viroids and satellite RNAs currently reported infecting grapevines (*Vitis* spp.) worldwide and its insect or nematode vectors.

Potyviridae	*Potyvirus*	*Bean common mosaic virus* (BCMV)	Aphids
	Fabavirus	*Broad bean wilt virus* (BBWV)	Aphids
Secoviridae	*Nepovirus* (Subgroup A)	*Arabis mosaic virus* (ArMV)	Nematode
		Grapevine fanleaf virus (GFLV) +	Nematode
		Raspberry ringspot virus (RpRSV)	Nematode
		Tobacco ringspot virus (TRSV)	Nematode
	Nepovirus (Subgroup B)	*Tomato black ring virus* (TBRV)	Nematode
		Artichoke Italian latent virus (AILV)	Unknown
		Grapevine chrome mosaic virus (GCMV)	Unknown
	Nepovirus (Subgroup C)	*Blueberry leaf mottle virus* (BBLMV)	Unknown
		Grapevine Tunisian ringspot virus (GTRSV)	Unknown
		Tomato ringspot virus (ToRSV)	Nematode
		Peach rosette mosaic virus (PRMV)	Nematode
		Cherry leaf roll virus (CLRV)	Unknown
		Grapevine Bulgarian latent virus (GBLV)	Unknown
	Nepovirus unclassified	*Grapevine Anatolian ringspot virus* (GARSV)	Unknown
		Grapevine deformation virus (GDefV)	Unknown
	Secoviridae unclassified	*Strawberry latent ringspot virus* (SLRV)	Nematode
Tombusviridae	*Carmovirus*	*Carnation mottle virus* (CarMV)	Unknown
	Necrovirus	*Tobacco necrosis virus* D (TNV-D)	Unknown
	Tombusvirus	*Grapevine Algerian latent virus* (GALV)	Unknown
		Petunia asteroid mosaic virus (PAMV)	Unknown
Tymoviridae	*Maculavirus*	*Grapevine fleck virus* (GFkV) +	Unknown
		Grapevine Red Globe virus (GRGV) +	Unknown
	Marafivirus	*Grapevine rupestris vein feathering virus* (GRVFV) +	Unknown
		Grapevine asteroid mosaic-associated virus (GAMaV)	Unknown
		Grapevine Syrah virus -1 (GSyV-1) +	Unknown
Virgaviridae	*Tobamovirus*	*Tobacco mosaic virus* (TMV)	Absent
		Tomato mosaic virus (ToMV)	Absent
Reoviridae	und	*Grapevine Cabernet Sauvignon reovirus* (GCSV) +	Unknown
und	*Idaeovirus*	*Raspberry bushy dwarf virus* (RBDV)	Unknown
und	*Sobemovirus*	*Sowbane mosaic virus* (SoMV)	Unknown
und	und	Grapevine Ajinashika virus (GAgV)	Unknown
und	und	Grapevine stunt virus (GSV)	Unknown
und	und	Grapevine labile rod-shaped virus (GLRSV)	Unknown
und	und	Temperate fruit decay-associated virus (TFDaV) +	Unknown

continuation...

TABLE 1 - Viruses, viroids and satellite RNAs currently reported infecting grapevines (*Vitis* spp.) worldwide and its insect or nematode vectors.

Pospiviroidae	*Apscaviroid*	*Australian grapevine viroid* (AGVd)	Absent
		Grapevine latent viroid (GLVd)	Absent
		Grapevine yellow speckle viroid 1 (GYSVd-1) [+]	Absent
		Grapevine yellow speckle viroid 2 (GYSVd-2)	Absent
		Grapevine yellow speckle viroid 3 (GYSVd-3)	Absent
	Hostuviroid	*Hop stunt viroid* (HSVd) [+]	Absent
	Pospiviroid	*Citrus exocortis viroid* (CEVd) [+]	Absent
und	und	*Grapevine hammerhead viroid-like RNA* (GHVd)	Absent
und	*Satellite RNA* (Subgroup I)	*Grapevine Bulgarian latent virus satellite RNA* (satGBLV)	Unknown
		Satellite RNA of *Grapevine fanleaf virus* (satGFLV-PPE)	Unknown
		Grapevine fanleaf virus satellite RNA (satGFLV)	Nematode
		RNA satellite unnamed (Al Rwahnih et al., 2013a)	Unknown
und	und	LN33 stem grooving [+]	
und	und	Grapevine vein mosaic	
und	und	Grapevine enation	
und	und	Grapevine summer mottle	

[+] Viruses, viroids and virus-like disease reported in Brazil infecting grapevines; und: taxonomy undetermined (ICTV Official Taxonomy, 2015). Adapted from MARTELLI (2014).

TABLE 2- Grapevine viruses and viroids reported in Brazilian vineyards and molecularly characterized.

Virus/ viroid	Genome portion	Nucleotide (bp)	GenBank accession (isolate)	References
GVA	Coat protein	597	AF494187 (Brazil), KF667501 (IT-BA), AY340581 (SP)	FAJARDO et al., 2003 MOREIRA et al., 2004b
	Coat protein	451	HM358052 (PC40), KJ848782 (NiagRos2), KJ848783 (NiagRos10)	BASSO et al., 2010a
GVB	Coat protein	594	AF438410 (BR1), KF040331 (CO), KF040332 (IS-SVF), KF040333 (CS), AY340582 (Common), AY340583 (Italia)	NICKEL et al., 2002 MOREIRA et al., 2004a CATARINO et al., 2015
GVD	Coat protein and RNA-binding protein	852	JQ031715 (Dolc) JQ031716 (Garg)	FAJARDO et al., 2012
GLRaV-1	Coat protein	969	GQ332536 (PS)	FAJARDO et al., 2011
GLRaV-2	Coat protein	597	EU053125 (M/C), EU053126 (L/I), EU204909 (SE), EU204910 (IT), EU204911 (MH), EU204912 (RI)	RADAELLI et al., 2009
	Coat protein	431	HM059035 (CS2), HM358050 (IS3)	BASSO et al., 2010a
	Coat protein	397	KJ958525 (Mer8), KJ958526 (Mer31)	CATARINO et al., 2015
	HSP70	596-623	HM059039 (CS1), HM130523 (SE)	BASSO et al., 2010a

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TABLE 2- Grapevine viruses and viroids reported in Brazilian vineyards and molecularly characterized.

GLRaV-3	Coat protein	942	DQ680141 (Pet-1), DQ680142 (Pet-2), DQ062152 (Pet-3), AY753208 (Pet-4), HM059034 (IS2), KJ704369 (RC-PE)	FAJARDO et al., 2007b BASSO et al., 2010a
	Replicase	340	AF438411 (Pet-4)	FAJARDO et al., 2002
	HSP70	593	HM059040 (IS1)	BASSO et al., 2010a
	HSP70	230	KC519443 (Pet-4)	FAJARDO et al., 2007b
GLRaV-4	HSP70	302	KC202814 (RB), KC202815 (ME)	CATARINO et al., 2015
GLRaV-4, strain 5	Coat protein	798	JQ821315 (Card5)	FAJARDO et al., 2012
	HSP70	565	JQ821314 (Card5)	FAJARDO et al., 2012
GLRaV-4, strain 6	HSP70	591	JQ290111 (Card)	FAJARDO et al., 2012
GRSPaV	Coat protein	780	EF636803 (CF195), EF636804 (CF207), EF690380 (MG), EF690381 (PN), EF690382 (MH), EF690383 (CF208), EF690384 (CF210), EU040204 (420A), EU204913 (CF195-2), GU166289 (CS1), GU166290 (IS2a), DQ443732 (SP), KJ848784 (NiagRos4), KJ848785 (NiagRos5), KT008367 to KT008381	PEREIRA, 2008 RADAELLI et al., 2009 BASSO et al., 2010a FAJARDO et al., 2015c
	Replicase	828-831	AY244640 (Sout. Brazilian), HM059036 (CS2a), HM059037 (IS1), AY340585	ESPINHA et al., 2003 FAJARDO et al., 2004 BASSO et al., 2010a
		339	HM059038 (CS2b), HM358051 (IS2b)	BASSO et al., 2010a
		628	HM130524 (IS3)	BASSO et al., 2010a
	Partial genome	8716	KT948710 (VF1)	FAJARDO et al., 2015c
GFLV	Coat protein	1515	EU258680 (RUP), EU258681 (IAC), EU038294 (RS)	RADAELLI et al., 2009
	Coat protein	321	AF418579 (RS)	FAJARDO et al., 2000
GFkV	Coat protein	693	JN022610 (BF)	FAJARDO et al., 2012
GRVFV	Coat protein	474	KC815703 (MER), KC815704 (SEM)	CATARINO et al., 2015
TFDaV	Complete genome	3442	KJ955449 (MFB15S1), KR134350 (MFB15S2)	BASSO et al., 2015
GVCV	Polyprotein	472	KR107537 (CS-BR)	FAJARDO et al., 2015c
GRGV	Coat protein	319	KR107538 (CS-BR)	
GSyV-1	Partial genome	6438-6465	KR153306 (VF-BR), KT037017 (MH), KX130754 (TRAJ-BR)	
	Coat protein	627	KX258763-KX258767	
GCSV	Partial genome	1110-3849	KR107527 to KR107536 (CS-BR)	FAJARDO et al., 2015a
	P4 protein	386	KR074408 (CS-BR)	
EVd	Complete genome	369-371	DQ444473 (CSC07), DQ444474 (NiagD11), DQ471994 (CSC09), DQ471995 (CSC10), DQ471996 (CSC11)	EIRAS et al., 2006

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TABLE 2- Grapevine viruses and viroids reported in Brazilian vineyards and molecularly characterized.

GYSVd-1	Complete genome	366-367	KU668661-KU668665, KU880712-KU880717	FAJARDO et al., 2015b
HSVd	Complete genome	297	DQ444475, DQ444476, DQ471997, DQ471998	EIRAS et al., 2006

GVA: *Grapevine virus A*; GVB: *Grapevine virus B*; GVD: *Grapevine virus D*; GLRaV: *Grapevine leafroll-associated virus*; GRSPaV: *Grapevine rupestris stem pitting-associated virus*; GFLV: *Grapevine fanleaf virus*; GFkV: *Grapevine fleck virus*; GRVFV: *Grapevine rupestris vein feathering virus*; TFDaV: Temperate fruit decay-associated virus; GVCV: *Grapevine vein clearing virus*; GRGV: *Grapevine Red Globe virus*; GSyV-1: *Grapevine Syrah virus-1*; GCSV: Grapevine Cabernet Sauvignon reovirus; CEVd: *Citrus exocortis viroi* GYSVd-1: *Grapevine yellow speckle viroid-1*; HSVd: *Hop stunt viroid*.

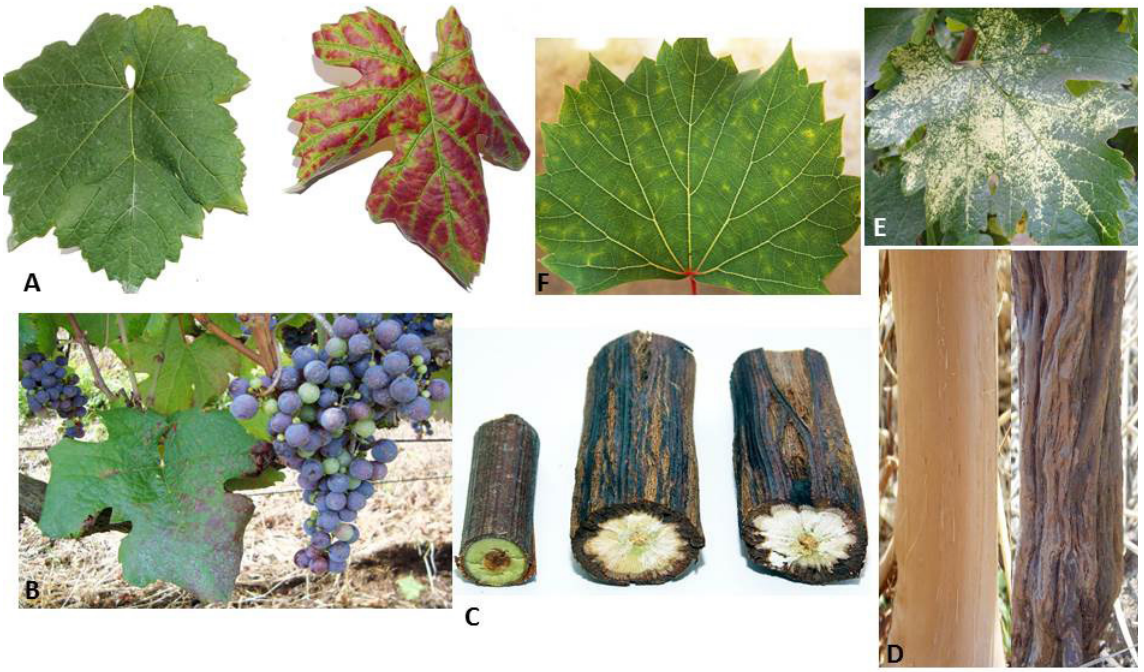

FIGURE 1-Symptoms observed in some grapevine cultivars in Brazilian vineyards: leaf without (left) and with typical symptoms (right) of grapevine leafroll (**A**) and lack of color in red grapes caused by this disease (**B**); corky bark in *V. labrusca* cv. Niagara Rosada (**C**) and stem pitting in rootstock cv. Paulsen 1103 (**D**) caused by rugose wood complex (healthy grapevines in left side of pictures); fanleaf degeneration (**E**); and fleck disease in grapevine (*Vitis rupestris* St. George) (**F**). **Photos:** Thor V. M. Fajardo.

TABLE 3- Some insect and nematode vectors of the viruses reported in Brazilian vineyards.

Vector	Grapevine virus diseases																		
	Leafroll disease						Rugose wood complex				Leaf degeneration	Fleck disease		Fruit tree decay	Redglobe disease	Syrah decline	Vein clearing	und	
	GLRaV																		
Mealybugs (*Pseudococcidae*)	**1**	**2**	**3**	**4**	**5***	**6***	**GVA**	**GVB**	**GVD**	**GRSPaV**	**GFLV**	**GFkV**	**GRVFV**	**TFDaV**	**GRGV**	**GSyV-1**	**GVCV**	**GCSV**	**References**
Heliococcus bohemicus	x		x				x												TSAI et al., 2010
Phenacoccus aceris	x		x	x	x	x	x	x											LE MAGUET et al., 2012; TSAI et al., 2010
Planococcus citri	x		x				x	x											TSAI et al., 2010; BERTIN et al., 2016
Planococcus ficus	x		x	x	x		x	x											TSAI et al., 2010
Pseudococcus viburni			x				x	x											TSAI et al., 2010
Pseudococcus calceolariae			x																TSAI et al., 2010
Pseudococcus comstocki			x				x												DAANE et al., 2012
Pseudococcus affinis							x	x											GARAU et al., 1995
Pseudococcus longispinus			x		x		x	x											TSAI et al., 2010
Pseudococcus maritimus	x		x																TSAI et al., 2010
Soft scales (*Coccidae*)																			
Neopulvinaria innumerabilis							x												FORTUSINI et al., 1997
Parthenolecanium corni	x		x				x												HOMMAY et al., 2008
Pulvinaria vitis	x		x																BELLI et al., 1994
Pulvinaria innumerabilis	x		x																FORTUSINI et al., 1997
Ceroplastes rusci			x		x														MAHFOUDHI et al., 2009
Coccus longulus			x																KRÜGER; DOUGLAS-SMIT, 2013
Coccus hesperidum			x																KRÜGER; DOUGLAS-SMIT, 2013
Parasaissetia nigra			x																KRÜGER; DOUGLAS-SMIT, 2013
Saissetia sp.			x																KRÜGER; DOUGLAS-SMIT, 2013
Nematodes																			
Xiphinema index											x								DAS; RASKI, 1968
Xiphinema italiae											x								COHN et al., 1970
Unknown vector		x							x	x		x	x	x	x	x	x	x	MARTELLI, 2014

GLRaV: *Grapevine leafroll-associated virus* (5* and 6*: strains of GLRaV-4); GVA: *Grapevine virus A*; GVB: *Grapevine virus B*; GVD: *Grapevine virus D*; GRSPaV: *Grapevine rupestris stem pitting-associated virus*; GFLV: *Grapevine fanleaf virus*; GFkV: *Grapevine fleck virus*; GRVFV: *Grapevine rupestris vein feathering virus;* TFDaV: Temperate fruit decay-associated virus; GRGV: *Grapevine Red Globe virus*; GSyV-1: *Grapevine Syrah virus-1*; GVCV: *Grapevine vein clearing virus*; GCSV: Grapevine Cabernet Sauvignon reovirus; und: undetermined.

CONCLUSION AND FUTURE PROSPECTS

The main prophylactic measure for the control of grapevine viruses is the use of propagation material free of viruses. Pathogen-derived resistance or transgenic technologies can provide means to achieve resistance in grapevine hybrids or rootstocks. However they are far from being widely established commercially. The utilization of NGS associated with expertise in bioinformatics is a powerful tool to investigate the grapevine virome. Several new pathogenic agents were recently identified and associated with important grapevine diseases. The application of these knowledge and technologies in grapevine quarantine and certification programs can improve the efficiency of these programs, contributing to control viral diseases worldwide.

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