INTRODUCTION

The grapevine (*Vitis* spp.) undoubtedly represents one of the woody crops most widely grown in temperate climates, and a highly valuable agricultural commodity. As most of the vegetatively propagated crops, grapevines are exposed to the attacks of a variety of pests and pathogens among which infectious intracellular agents (viruses, viroids, phloem- and xylem-limited prokaryotes) play a major role, causing heavy losses, shortening the productive life of vineyars, and endangering the survival itself of affected vines. The importance of the grapevine industry and the magnitude of the problems caused by these pathogens has generated wide interest which, in turn, has fostered intensive research which has been especially active at the international scale from the late 1950's onwards. The increased attention paid to grapevine's virological problems and the like has produced an impressive series of papers which now number over 5,000. The papers up to 2003 are listed and commented in six bibliographic reports:

– Caudwell A., 1965. Bibliographie des viroses de la vigne des origines à 1965. Office International de la Vigne et du Vin, Paris, 76 pp.;
– Caudwell A., Hewitt W.B., Bovey R., 1972. Les virus de la vigne. Bibliographie de 1965-1970. *Vitis* **11**: 303-324;
– Hewitt W.B., Bovey R., 1979. The viroses and virus-like diseases of the grapevine. A bibliographic report 1971-1978. *Vitis* **18**: 316-376;
– Bovey R., Martelli G.P., 1986. The viroses and virus-like diseases of the grapevine. A bibliographic report 1979-1984. *Vitis* **25**: 227-275;
– Bovey R., 1999. The viroses and virus-like diseases of the grapevine: bibliographic report 1985-1997. *Options Méditerranéenes* **29** (Series B, 3rd part): 8-172;
– Bovey R., 2006. The viroses and virus-like diseases of the grapevine. A bibliographic report 1997-2003. *Options Méditerranéennes* **29** (Series B, 3rd part): 7-172.

which have been compiled under the auspices of the International Council for the Study of Viruses and Virus Diseases of the Grapevine (ICVG).

ICVG was established in 1962 by a group of American and European plant pathologists who realized the importance of creating an international organization for promoting research on grapevine virology and favouring the exchange of information among researchers (Bovey R., Gugerli P., 2003. A short history of ICVG. *Extended Abstracts 14th Meeting of ICVG, Locorotondo, Italy:* 1-2).

Since its foundation, ICVG has met at:

1. Changins (Switzerland), 17-20 August 1964
2. Davis (California, USA), 7-11 September 1965
3. Bernkastel-Kues (West Germany), September 1967
4. Colmar (France), 16-18 June 1970
5. Salice Terme (Italy), 16-19 September 1973
6. Cordoba and Madrid (Spain), 12-17 September 1976
7. Niagara Falls (Ontario, Canada), 7-12 September 1980
8. Bari (Italy), 2-7 September 1984
9. Kiryat Anavim (Israel), 6-11 September 1987
10. Volos (Greece), 3-7 September 1990
11. Montreux (Switzerland), 5-10 September 1993
12. Lisbon (Portugal), 28 September - 2 October 1997
13. Adelaide (South Australia), 12-17 March 2000
14. Locorotondo (Italy), 12-17 September 2003
15. Stellenbosch (South Africa), 3-7 April 2006
16. Dijon (France), 31 August - 4 September 2009
17. Davis (California, USA), 7-14 October 2012
18. Ankara (Turkey), scheduled for 7-11 September 2015

From the very beginning, ICVG has been instrumental in fostering basic and applied research in grapevine virology, attracting the attention of scientists, growers, nurserymen and administrators on the detrimental effects of infectious diseases on the well-being of the industry, and supporting initiatives for the establishment and implementation of clean stock programmes and certification schemes.

To this effect, among other things, ICVG has issued the recommendations that follow:

> *The International Council for the Study of Viruses and Virus Diseases of the Grapevine (ICVG), recognizes that a number of the 60 or so infectious agents (viruses, viroids, and phytoplasmas) recorded from the grapevine can be highly detrimental to this crop, having a negative impact on the plant vigour and longevity, as well as on the quality and quantity of the yield. Infected propagating material is largely responsible for the spread of diseases among and within viticultural countries. Thus, all efforts should be made to improve its sanitary conditions.*

The presence of diseases such as infectious degeneration, leafroll, rugose wood, and fleck, is regarded as incompatible with an accepted sanitary status. Their elimination from mother vines intended for propagation should therefore be pursued.
Improvement of the sanitary level can be achieved through selection and sanitation, which are best performed in the framework of certification programmes encompassing also clonal selection.
(Approved in 1997 at the 12th ICVG Meeting, Lisbon, Portugal)

The International Council for the Study of Virus and Virus-like Diseases of the Grapevine (ICVG), recognises over 70 infectious agents affecting grapevine (viruses, viroids and phytoplasmas), many of which can be highly detrimental to this crop, having a negative impact on plant vigour and longevity, as well as on the quality and quantity of the yield. Certification of grapevine nursery stock is a powerful and effective tool to control these agents, that enables vineyards to economically and sustainably maintain quality and productivity. Certified grapevines are derived from pathogen tested, clonally selected primary sources. The certification process should specify conditions to prevent and detect subsequent infection of nursery plants by regulated pests, ensure clonal integrity, and permit tracing the certified grapevines to the originally selected and tested plants.
Inadequate certification standards have repeatedly resulted in disease problems for growers and nurserymen. Infected propagation material is largely responsible for the spread of diseases among and within viticultural countries. Thus, all efforts should be made to improve its sanitary conditions. However, valuable grape genetic resources exist which are infected with virus but are essential to the preservation of world viticultural heritage.
In order to preserve valuable grape clones and varieties, we propose two sanitary classes. Certified selections should be tested for specific pathogens. Class 1 should include only grape nursery stock which tests negative for the most damaging diseases/pathogens. It would move freely between regulatory boundaries. Class 2 would be a specific pathogen-tested certification system for stock which remains within regulatory regions and is only distributed with disclosure of health status. No other stock should move outside regulatory regions.
The agents that should be controlled by the Class 1 certification program are those associated with infectious degeneration and grapevine decline (nepoviruses); leafroll disease and associated closteroviruses (grapevine leafroll associated viruses 1, 2, and 3); rugose wood (GVA, GVB and GVD); and phytoplasmas (flavescence dorée, bois noir, and other grapevine yellows).In the future, technology should make it possible to exclude additional disease-causing viruses from the certified stock, including the causal agents of fleck and rupestris stem pitting. Until that time, a moratorium will be established for these viruses.
The regional certification standards for Class 2 stock should be created at a local level based on the rate of endemic infection, regional viticultural conditions, and the need for preservation of heritage germplasm. As efforts are made to harmonize grapevine certification protocols, high standards are essential to ensure that no viticultural area is compromised by the introduction and spread of diseases.
(Approved in 2003 at the 14th ICVG Meeting, Locorotondo, Italy)

The International Council for the Study of Virus and Virus-like Diseases of the Grapevine (ICVG) recognizes over 75 infectious agents (viruses, viroids, and phytoplasmas) affecting grapevine. These pathogens are graft-transmissible and many can be highly detrimental, having a negative impact on plant vigor and longevity, as well as on fruit quality and quantity.
Infected propagation material is the primary means for the spread of graft-transmissible diseases among countries and within viticultural regions. Therefore, all efforts should be made to improve its sanitary condition. Certification is a powerful and effective strategy to control these graft-transmissible agents and promote the quality, profitability and sustainability of vineyard production.
Certified grapevines are derived from pathogen-tested, clean and clonally selected nursery stocks. The certification process makes provisions to identify clean stocks, prevent and detect subsequent infection of nursery plants by regulated pathogens and pests, ensure clonal integrity, and permit traceability of the certified grapevines to the originally selected and tested stocks.
High standards are paramount for certification to be efficient, as inadequate standards have repeatedly resulted in disease problems for growers and nurserymen. Certified nursery stocks should test negative for the most damaging diseases/pathogens to be eligible to move between regulated areas under the control of individual National Plant Protection Organizations.
The agents that should be controlled by certification programs are those associated with infectious degeneration and decline (nepoviruses), leafroll disease and all associated viruses (Grapevine leafroll-associated viruses 1, 2, 3, 4 and 7), rugose wood and some of the associated vitiviruses (Grapevine virus A and grapevine virus B), and phytoplasmas (Flavescence dorée, Bois noir, and other grapevine yellows). In the future, the fast advancing diagnostic technologies will make it possible to exclude additional disease causing viruses from certified stocks, including other viurses associated with the rugose wood disease, marafiviruses and maculaviruses associated with the fleck disease complex, betaflexiviruses associated with rupestris stem pitting disease and vein necrosis complexes, as well as other new viruses associated with emerging diseases. Until that time, a moratorium will be established for these viruses.
As efforts are made to harmonize grapevine certification protocols across countries or viticulture regions, while preserving genetic resources that are part of the world viticultural heritage, high standards are essential to ensure that no viticultural area is compromised by the introduction and spread of graft-transmissible diseases.
(approved in 2012 at the 17th ICVG Meeting, Davis, CA, USA)

These recommendations were and are intended to inform regulators on the current status of the knowledge on infectious diseases of grapevines, in the hope that they could serve as guidelines when sanitary provisions for the production and marketing of propagative material (nursery

productions) are to be issued by countries hosting relevant viticultural industries.

It is unfortunate that little or no attention was paid to them by the Commission of the European Community (EU) when it decided to revise the Directive 68/193/CEE, issued in 1968, on the "Marketing of materials for the vegetative propagation of the grapevine". This Directive classified these materials in three categories "basic", "certified" and "standard" and contained the following sanitary provisions: (i) *When nurseries of mother vine plots for the production of "basic" and "certified" propagating material are established, the highest possible guarantee must exist that the soil in not infected by harmful organisms, viruses in particular;* (ii) *In these vineyards the presence of harmful organisms which reduce the value of propagative material is tolerated only within the narrowest possible limit*"*;* (iii) *These vineyards must be kept free from plants showing symptoms of virus diseases.*

Over time, Directive 68/193/CEE was revised twice. The first amendment (Directive 71/140/EC), stated that: "*In the vineyards producing "basic" material, harmful virus diseases, notably fanleaf and leafroll, must be eliminated. Vineyards producing material of other categories must be kept free from plants showing symptoms of virus diseases.* The second and last (Directive 2005/43/EC) affirmed that *"The presence of harmful organisms which reduce the usefulness of the propagation material shall be at the lowest possible level*", specifying that the "*lowest possible level"* consisted in the absence of:

i. Complex of infectious degeneration: *Grapevine fanleaf virus* (GFLV) and *Arabis mosaic virus* (ArMV)

ii. Grapevine leafroll disease: *Grapevine leafroll-associated virus 1* (GLRaV-1) and *Grapevine leafroll-associated virus 3* (GLRaV-3)

iii. *Grapevine fleck virus* (GFkV) (only for rootstocks)

Apart from the extravagant decision of tolerating GFkV infections in the scions from which, in grafted plants, the virus would move anyhow to the GFkV-free rootstocks, no mention was made of *Grapevine leafroll-associated virus 2* (GLRaV-2) which, together with its RG strain, is unanimously recognized as a most insidious inducer of graft incompatibility, nor of any of the viruses of the rugose wood complex.

The ICVG recommendation issued in 2003 at Locorotondo, and a former proposal for a certification scheme elaborated by a panel of European virologists members of ICVG (see: Martelli G. P., De Sequeira O.A., Kassemeyer H.H., Padilla V., Prota U., Quacquarelli, A., Refatti E., Rudel M., Rumbos I.C., Savino V., Walter B., 1993. A scheme for grapevine certification in the European Economic Community. *British Crop Protection Council Monograph* **54:** 279-284), both of which had been circulated among representatives of the Ministries of Agriculture of EU Member States and forwarded to the EU officials who were in charge of the negotiations for the annexes to the Directive, were totally disregarded. The ultimate result is that, because of the enforcement of Directive 2005/43/EC, the EU grapevine nursery industry is allowed to produce and release "certified" material with a lamentably low sanitary standard.

However, since the EU Directive can be interpreted as setting minimal sanitary standards, the Italian conservative breeders (obtenteurs) have signed an agreement, endorsed by the Ministry of Agriculture, whereby GLRaV-2 and the rugose wood-associated viruses *Grapevine virus A* (GVA) and *Grapevine virus B* (GVB), but not *Grapevine rupestris stem pitting-associated virus* (GRSPaV), have been added to the list of pathogens whose absence from nursery productions must be certified.

The Proceedings of all the ICVG Conferences have been published and represent a most valuable source of information. In addition, the virological problems of grapevines have been extensively addressed and illustrated in a number of books:

– Uyemoto J.K, Martelli G.P., Woodham R.C., Goheen A.C., Dias H.F., 1978. Grapevine (*Vitis*) virus and virus-like diseases. In: Barnett O.W., Tolin S.A. (eds). Plant Virus Slide Series, Set 1. Clemson University, Clemson, USA.

– Bovey R., Gärtel W., Hewitt W.B., Martelli G.P., Vuittenez A., 1980. Virus and Virus-like Diseases of Grapevines. Editions Payot, Lausanne, Switzerland.

– Pearson R.G., Goheen A.C, 1988. Compendium of Grape diseases. APS Press, St. Paul, MN, USA, 93 pp. A second edition of this Compendium edited by W.F. Wilcok, W.D. Gubler and J.K. Uyemoto is scheduled for publication in 2014.

– Frison E.A., Ikin R., 1991. FAO/IBPGR Technical Guidelines for the Safe Movement of Grapevine Germplasm. FAO Publication Division, Rome, Italy.

– Martelli G.P. (ed.), 1993. Detection and Diagnosis of Graft-transmissible Diseases of Grapevines. FAO Publication Division, Rome, Italy.

– Krake L.R., Scott N.S., Rezaian M.A., Taylor R.H., 1999. Graft-transmissible Diseases of Grapevines. CSIRO Publishing, Collingwood, Australia.

– Walter B., Boudon-Padieu E., Ridé M., 2000. Maladies à Virus, Bactèries et Phytoplasmes de la Vigne. Editions Fèret, Bordeaux, France.

– Uyemoto J.K., Martelli G.P., Rowhani A., 2009. Grapevine viruses, viruslike diseases and other disorders. In: Virus Diseases of Plants: Grape, Potato and Wheat Image Collection and Teaching Resource CD-Rom. APS Press, St. Paul, MN, USA.

– Anonymous, 2012. *Vitis* (Grapevine) Post-Entry Quarantine Testing Manual. Ministry of Primary Industries. Plant Health and Environment Laboratory Investigation and Diagnostic Centres and Response, Auckland, New Zealand.

Great advances have also been made in diagnosis, especially with systems for screening propagative material that aim at the simultaneous detection of multiple viruses. One last example is the development of a crop-specific macroarray for the concomitant detection of 38 of the 65 or so known grapevine-infecting viruses, which represents the largest example of a reusable detection system for plant viruses (see Thompson J.R., Fuchs M., McLane H., Celebi-Toprak F., Fischer K.F., Potter J.L., Perry K.L, 2014. Profiling viral infections in grapevine using a random primes reverse transcription-polymerase chain reaction/macroarray multiplex platform. *Phytopathology* **104**: 211-219).

Notwithstanding this wealth of published information a "*Directory of Major Virus and Virus-like Diseases of Grapevines*" was compiled in 1992 by R. Bovey and G.P. Martelli and published under the auspices of the Mediterranean Fruit Crop Improvement Council (MFCIC), a body now estinguished, which was established in the framework of the International Project RAB/88 sponsored by the United States Development Programme and the Food and Agriculture Organization of the United Nations.

This Directory was updated in 2006 by G.P. Martelli and E. Boudon-Padieu and published in Options Méditerranéennes under the title of *"Directory of Infectious Diseases of Grapevines"*.

Thus, the current *"Directory of Virus and Virus-like Diseases of the Grapevine and their Agents"* represents the third edition of this endeavour which, like the former editions, is intended to serve as a useful guideline and working tool for both experienced researchers and those who are now approaching the fascinating field of grapevine virology.

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NEXT GENERATION SEQUENCING, A POWERFUL TOOL FOR THE DISCOVERY OF NEW GRAPEVINE-INFECTING VIRUSES

The identification of the putative marafivirus Grapevine Syrah virus 1 (GSyV-1) is the first example in grapevine virology of the application of a novel sequencing technology, referred to as "deep sequencing" or "high-throughput pyrosequencing", or "next generation sequencing (NGS)" which enables the recovery of hundred of thousand sequence fragments from total RNA extracts from diseased plants, that can derive from a multiplicity of viruses ("virome") and other pathogens present in the analyzed host. Other such NGS-mediated discoveries of hitherto unknow *Vitis*-infecting viruses are: (i) two putative badnaviruses one of which, denoted Grapevine vein clearing virus (GVCV) was identified in the USA whereas the other was found in Greece in vines affected by Roditis leaf discoloration; (ii) the trichovirus *Grapevine Pinot gris-associated virus* (GPGaV); (iii) the putative vitivirus Grapevine virus F (GVF); (iv) Grapevine red blotch-associated virus (GRBaV) a member of a putative new genus in the family *Geminiviridae*; (v) a novel satellite virus whose RNA bears no apparent relationship with any known plant virus genes. This is the beginning of what is likely to result into a possible long list of previously unrecorded grapevine-infecting viruses

HISTORICAL REVIEW

2009 **Al Rwahnih** *et al.*: Description of Grapevine Syrah virus 1 from California (USA). Virus detected also in the leafhopper *Erythroneura variabilis.*

2009 **Sabanadzovic** *et al.*: Description of Grapevine virus Q from muscadine and European grapes in Mississippi (USA). The virus is the same as GSyV-1.

2011 **Giampetruzzi** *et al.*: Description of *Grapevine Pinot gris-associated virus* (GPGaV) from northern Italy. The virus is phylogenetically close to *Grapevine berry inner necrosis virus* from Japan

2011 **Zhang** *et al.*: Description of Grapevine vein clearing virus (GVCV) from grapevines in the US Midwest, the first DNA virus found in *Vitis.*

2012 **Al Rwahnih** *et al.*: Description of Grapevine virus F from California (USA).

2012 **Krenz** *et al.*: Description of Grapevine Cabernet franc-associated virus (GCFaV) from New York state (USA), the second DNA virus found in *Vitis.*

2012 **Al Rwahnih** *et al.*: Identification of DNA virus in vines from California (USA) showing a red blotch syndrome. Virus is the same as Grapevine Cabernet franc-associated virus but was called Grapevine red blotch-associated virus (GRBaV), the likely ultimate denomination.

2013 **Al Rwahnih** *et al.*: Identification in grapevines from California (USA) of the sequence of an unidentified plant virus satellite.

2013 **Poojari** *et al.*: Identification in grapevines from Washington state (USA) and transmission by the leafhopper *Erythroneura ziczac* of a DNA virus identical to that already described from New York state and California. Virus given a third non adopted denomination, i.e. Grapevine redleaf-associated virus.

2014 **Maliogka and Katis**: A putative badnavirus identified in vines affected by Roditis leaf discoloration

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Al Rwahnih M., Dave A., Anderson M., Uyemoto J.K., Sudarshana M.R., 2012. Association of a circular DNA virus in grapevines affected by the red blotch disease in California. *Proceedings 17th Meeting of ICVG, Davis, CA, USA*: 104-105.

Al Rwahnih M., Daubert S., Sudarshan M.R., Rowhani A., 2013. Gene from a novel plant virus satellite from grapevine identifies a satellite lineage. *Virus Genes* 47: 114-118.

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Krenz B., Thompson J.R., Fuchs M., Perry K.L., 2012. Complete

genome sequence of a new circular DNA virus from grapevine. *Journal of Virology* **86**: 7715.

Maliogka V., Katis N., 2014. Personal communication.

Poojari S., Alabi O.J., Fofanov V.Y., Naidu R.A., 2013. A leafhopper-transmissibile DNA virus with novel evolutionary lenage in the family *Geminiviridae* implicated in grapevine readleaf disease by next-generation sequencing. *PLOS ONE* **8**: e64194

Sabanadzovic S., Abou Ghanem-Sabanadzovic N., Gorbalenya A.E., 2009. Grapevine virus Q: the first plant virus with a permuted active site of a RNA-dependent RNA polymerase. *Extended Abstracts 16th Meeting of ICVG, Dijon, France*: 42-43.

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GRAPEVINE-INFECTING VIRUSES

More than 70 infectious agents among viruses (65), viroids (5), phytoplasmas (8), and insect-transmitted xylematic bacteria (1) have been recorded form grapevines. This represents the highest number of intracelluar pathogens ever found in a single crop.

Table 1. The viral scenario of *Vitis* and *Muscadinia*: viruses and their taxonomic affiliation[(a)]

FAMILY	GENUS	SPECIES
A. Viruses belonging to genera included into families		
Viruses with a single-stranded DNA genome		
GEMINIVIRIDAE	Undetermined	Grapevine Cabernet franc-associated virus (GCFaV)
Viruses with a double-stranded DNA genome		
CAULIMOVIRIDAE	*Badnavirus*	Grapevine vein clearing virus (GVCV). An unnamed virus from vines affected by Roditis leaf discoloration
Viruses with a double-stranded RNA genome		
REOVIRIDAE	*Oryzavirus*	Unnamed virus
ENDORNAVIRIDAE	*Endornavirus*	Two unnamed viruses
PARTITIVIRIDAE	*Alphacryptovirus*	Raphanus sativus cryptic virus 3 (RsCV-3) like Beet cryptic virus 3 (BCV-3) like
Viruses with a negative-sense single-stranded RNA genome		
BUNYAVIRIDAE	*Tospovirus*	*Tomato spotted wilt virus* (TSWV)
Viruses with a positive-sense single-stranded RNA genome (filamentous particles)		
CLOSTEROVIRIDAE	*Closterovirus*	*Grapevine leafroll-associated virus 2* *(GLRaV-2)*
	Ampelovirus	*Grapevine leafroll-associated virus 1* (GLRaV-1) *Grapevine leafroll-associated virus 3* (GLRaV-3) *Grapevine leafroll-associated virus 4* (GLRaV-4) GLRaV-4 strain 5 GLRaV-4 strain 6 GLRaV-4 strain 9 GLRaV-4 Pr GLRaV-4 strain Car
	Velarivirus	Grapevine leafroll-associated virus 7 (GLRaV-7) r
ALPHAFLEXIVIRIDAE	*Potexvirus*	*Potato virus X (PVX)*
BETAFLEXIVIRIDAE	*Foveavirus*	*Grapevine rupestris stem pitting-associated virus* (GRSPaV)
	Trichovirus	*Grapevine berry inner necrosis virus* (GINV) *Grapevine Pinot gris virus* (GPGV)
	Vitivirus	*Grapevine virus A* (GVA) *Grapevine virus* B (GVB) *Grapevine virus D* (GVD) *Grapevine virus E* (GVE) Grapevine virus F (GVF)
POTYVIRIDAE	*Potyvirus*	Unidentified potyvirus-like virus isolated in Japan from a Russian cv. *Bean common mosaic virus* (BCMV), peanut strain

Viruses with a positive-sense single-stranded RNA genome (rod-shaped particles)			
VIRGAVIRIDAE	*Tobamovirus*	*Tobacco mosaic virus* *Tomato mosaic virus*	(TMV) (ToMV)
Viruses with a positive-sense single-stranded RNA genome (isometric particles)			
SECOVIRIDAE	*Fabavirus*	*Broadbean wilt virus*	(BBWV)
	Nepovirus	*Artichoke italian latent virus* *Arabis mosaic virus* *Blueberry leaf mottle virus* *Cherry leafroll virus* *Grapevine Bulgarian latent virus* *Grapevine Anatolian ringspot virus* *Grapevine deformation virus* *Grapevine chrome mosaic virus* *Grapevine fanleaf virus* *Grapevine Tunisian ringspot virus* *Peach rosette mosaic virus* *Raspberry ringspot virus* *Tobacco ringspot virus* *Tomato ringspot virus* *Tomato blackring virus*	(AILV) (ArMV) (BBLMV) (CLRV) (GBLV) (GARSV) (GDefV) (GCMV) (GFLV) (GTRV) (PRMV) (RpRSV) (TRSV) (ToRSV) TBRV)
	Unassigned in the family	*Strawberry latent ringspot virus*	(SLRSV)
BROMOVIRIDAE	*Alfamovirus*	*Alfalfa mosaic virus*	(AMV)
	Cucumovirus	*Cucumber mosaic virus*	(CMV)
	Ilarvirus	Grapevine line pattern virus Grapevine angular mosaic virus	(GLPV) (GAMoV)
TOMBUSVIRIDAE	*Carmovirus*	*Carnation mottle virus*	(CarMV)
	Necrovirus	*Tobacco necrosis virus D*	(TNV-D)
	Tombusvirus	*Grapevine Algerian latent virus* *Petunia asteroid mosaic virus*	(GALV) (PAMV)
TYMOVIRIDAE	*Marafivirus*	*Grapevine asteroid mosaic-associated virus* Grapevine redglobe virus Grapevine Syrah virus 1 Blackberry virus S Unnamed putative marafivirus-like virus	(GAMaV) (GRGV) (GSV-1) (BlVS)
	Maculavirus	*Grapevine fleck virus* Grapevine rupestris vein feathering virus	(GFkV) (GRVFV)
B. Viruses belonging to genera unassigned to families			
	Idaeovirus	*Raspberry bushy dwarf virus* (RBDV)	
	Sobemovirus	*Sowbane mosaic virus* (SoMV)	
C. Taxonomically unassigned viruses			
		Unnamed filamentous virus	
		Grapevine Ajinashika virus	(GAgV)
		Grapevine stunt virus	(GSV)
		Grapevine labile rod-shaped virus	(GLRSV)
		Southern tomato virus	(STV)

[(a)] Scientific names of definitive virus species are written in *italics*. The names of tentative species are written in Roman characters. The updated taxonomy of all classified grapevine viruses can be found in King A.M.Q, Adams M.J., Carstens E.B., Lefkowitz E.J. 2011. IX Report of the International Committe on Taxonomy of Viruses Elsevier-Academic Press, Amsterdam, The Netherlands. This table comprises also the new viruses reported from south-eastern USA a detailed description of which has not yet been published.

INFECTIOUS DEGENERATION

INFECTIOUS DEGENERATION (*GRAPEVINE FANLEAF VIRUS*)

Several nepoviruses infect grapevines in Europe and the Mediterranean area, causing degenerative diseases whose symptoms are similar to, or indistinguishable from those of fanleaf, a disorder induced by the nepovirus *Grapevine fanleaf virus* (GFLV). This name comes from the peculiar malformation of infected leaves that exhibit widely open petiolar sinuses and abnormally gathered primary veins giving the leaf the appearance of an open fan. GFLV and several of the other grapevine-infecting European nepoviruses have distorting and chromogenic strains and may occur in mixed infections. Their economic impact varies with the tolerance of the cultivar to the individual viruses. Tolerant cultivars produce fairly good crops whereas the sensitive ones are severely affected, showing progressive decline of the vines, low yields and low fruit quality, shortened productive life, low proportion of graft take, reduced rooting ability of propagation material, and decreased resistance to adverse climatic factors.

FANLEAF

1. DESCRIPTION.

Fanleaf is the oldest known and one of the most important and widespread virus disease of the grapevine. In the European literature, records of this disease date back some 150 years, and grapevine leaves with typical symptoms are contained in herbaria established before the introduction of American rootstock hybrids. The consensus is that fanleaf degeneration may have existed in the Mediterranean basin and the Near East since the earliest time of grape cultivation. Now the disease is known to occur worldwide.

Main synonyms: court-noué, panachure, dégénérescence infectieuse (Fr.), roncet, arricciamento, mosaico giallo, degenerazione infettiva (Ital.), urticado (Port.), Reisigkrankheit (partly), Gelbmosaik (Germ.).

Main symptoms: Two distinct syndromes caused by different strains of the causal agent characterize this disease.

– *Infectious malformations* are induced by "distorting" virus strains. Leaves are variously and more or less severely malformed, asymmetrical, puckered, may show open petiolar sinuses, deep lobes, and acute denticulations. Occasionally, chlorotic mottling may accompany foliar deformations. Shoots are also malformed, showing abnormal branching, double nodes, short internodes, fasciations, and zigzag growth. Bunches are smaller and fewer than normal, and berries ripen irregularly, are small-sized and set poorly. Foliar symptoms develop early in the spring and persist throughout the vegetative season becoming less distinct in summer.

– *Yellow mosaic* is induced by chromogenic virus strains. The foliage develops bright chrome yellow discolorations early in the spring that may affect all vegetative parts (leaves, shoots, tendrils, and inflorescences). Chromatic alterations of the leaves vary from a few scattered yellow spots, sometimes appearing as rings or lines, to extensive mottling of the veins and/or interveinal areas, to total yellowing. Often infected grapevines occur in patches The foliage and shoots show little if any malformation, but bunches are small and few. With increased ambient temperatures during summer, the yellowing fades away and the canopy develops a normal green color. Recombination analysis predicted potential recombination events with *Arabis mosaic virus* (ArMV) in the $2A^{HP}$ gene encoding the "homing protein" in numerous virus isolates recovered from vines with yellow mosaic symptoms.

The characterizing symptoms of "*Vein banding*", another disease sometimes found in vineyards affected by infectious degeneration, consist of chrome yellow flecks first localized along the main veins of mature leaves and progressing into the interveinal areas. This type of discoloration appears in mid to late summer in a limited number of leaves which show little or no malformation. Fruit set is poor, bunches are straggly, and the yield may be much reduced. This disorder was first described in California as a syndrome elicited by a specific GFLV strain. More recently, however, the vein banding condition has been shown to be caused by a co-infection by Grapevine yellow speckle viroids and GFLV.

Trabeculae, or endocellular cordons, are radial bars crossing the lumen of epidermal, parenchyma, phloem, and xylem cells. They are oustanding in tracheary elements, their presence being a diagnostic GFLV marker. These structures can be observed by light microscopy in lignified shoots, especially in the basal internodes.

Agent: *Grapevine fanleaf virus* (GFLV) is a nepovirus with polyhedral particles of about 30 nm in diameter, serologically very uniform, and occurring as a family of minor molecular variants. The genome is a positive-sense single-stranded RNA consisting of two functional molecules with mol wt. of 2.4×10^6 and a size of 7,342 nt (RNA-1) and 1.4×10^6 and a size of 3,774 nt (RNA-2), which are both required for infectivity and are encapsidated in different particles. RNA species are translated into polypeptides with a size of 2,284 aa and mol wt. of 253 kDa (RNA-1) and mol wt. of 131 kDa (RNA-2), respectively. These polypeptides are cleaved by a RNA-1- encoded viral protease., The primary structure of the RNA-1-encoded polyprotein comprises, in the 5' to 3' direction, a putative RNA-dependent RNA polymerase (M_r 92 kDa) followed by a cystein protease (M_r 25 kDa), the genome-linked protein (VPg, M_r 3 kDa), a 88 kDa protein containing the signature of a a nucleotide-binding domain and a protease cofactor, and a terminal protein 46 kDa in size. RNA-2 codes for the homing protein (M_r 28 kDa) implicated in RNA-2 replication, the 38 kDa movement protein and the coat protein (M_r 56 kDa). GFLV was the first grapevine virus to be recovered by mechanical inoculation and to be thoroughly characterized physico-chemically and molecularly. A satellite RNA of the nepoviral B type, 1104-1114 nt in size and encoding a 37 kDa protein called P3 is associated with some virus isolates (e.g. GFLV-F13 from France and GFLV-SACH44 from South Africa). These satRNAs do not seem to interfere with virus virulence and may have originated from recombination between an ancestal subgroup A [GFLV, *Arabis mosaic virus* (ArMV), *Grapevine deformation virus* (GDefV)] nepovirus RNA and an unknown RNA sequence.

Cytopathology: GFLV elicits the formation of intracellular cytopathic structures known as vesiculate-vacuolate inclusion bodies which are often apposed to the nucleus. These inclusions derive from cell membrane proliferation, reorganization, and redistribution and are thought to be sites of viral polyprotein processing and RNA replication. Virus particles are often present within tubular structures that accumulate in bundles in the cytoplasm or nucleus. Endocelluar cordons or "trabeculae" are abnormal straight cylindrical spool-like o ribbon-like structures of pectocellulosic nature that cross the cell lumen in different tissues and are especially oustanding in tracheids, where they occur in a radial orientation.

Transmission: At a site, in a persistent manner by the longidorid nematode *Xiphinema index* feeding on the roots of grapevines and retaining the virus for several months. Nematode populations transmit local virus isolates with a higher efficiency than those from other geographical areas. Specific transmission by *X. index* is determined by the viral coat protein. The sequence determining viral transmission consists of a stretch of 11 conserved amino acids located in an exposed region of the CP. The study of a poorly transmissible GFLV isolate showed that the transmission defect was due to a glycine/aspartate mutation in the CP (GFLV-TD). This mutation was localized on an exposed loop at the outer surface of the CP which did not affect the conformation of the capsid nor of individual CP subunits. This loop is part of a positively charged pocket that includes the 11 aa transmission determinant. The suggestion is that perturbation of the electrostatic landscape of this pocket affects the interaction of the virus particles with specific receptors in the nematode's feeding apparatus thus decreasing transmission efficiency. *X. index* populations from Cyprus, Israel, Italy, Spain, southern France, northern France and California showed remarkably different reproductive rates regardless of the grape genotypes (*Vitis rupestris* and *Vitis vinifera* cv. Cabernet sauvignon) on which they were reared. However, there was no differential vector competency among the seven above nematode lines in the transmission of two distinct GFLV strains (F13 and GHu). Transmission by *Xiphinema italiae* has not been consistently documented, and transmission by *X. vuittenezi* has been suspected but not proven. Dissemination over medium and long distances is through infected vegetatively propagated scionwood and rootstocks. In the laboratory, GFLV can be transmitted by mechanical inoculation from infected grapevine tissues to various herbaceous hosts (e.g. *Chenopodium quinoa*, *C. amaranticolor*, *Gomphrena globosa*). The virus occurs in the pollen of infected grapevine and herbaceous hosts, the endosperm of grapevine seeds, and is transmitted through seeds of *C. amaranticolor*, *C. quinoa*, and soybean. There are conflicting reports on seed transmission in grapevines. Natural GFLV infections have been detected in weeds in Hungary and Iran.

Varietal susceptibility: Almost all known *Vitis vinifera* L. varieties are susceptible, with variable levels of sensitivity. However, tolerance to infection is widespread in European grapes and a high resistance level of the "host plant resistance" type was found in two accessions from Afghanistan and Iran. This resistance is controlled by two unlinked recessive genes. American rootstocks are also susceptible and are generally very sensitive, although some like *Vitis labrusca* can be infected, but show few symptoms. *Muscadinia rotundifolia* and *Vitis munsoniana* are highly resistant to *X. index* feeding. *M. rotundifolia* can be infected by GFLV when graft inoculated, but resists infection when the virus is transmitted by the nematode. Resistance to *X. index* in *V. rupestris* x *M. rotundifolia* hybrids is thought to be controlled by a single dominant gene. Some *V. vinifera* × *M. rotundifolia* hybrid rootstocks (e.g. O36-16) show interesting levels of field resistance to GFLV. The resistance to *X. index* derived from *Vitis arizonica* is largely controlled by the quantitative trait locus XiR1 (*X. index* Resistance 1). The genetic map of this locus has been reconstructed and markers have been

developed that can expedite breeding of resistant grape rootstocks.

Geographical distribution: Worldwide

Detection: ELISA using polyclonal antisera and monoclonal antibodies is a quick, cheap, and very sensitive method. The best antigen sources for serological diagnosis are leaves collected in spring or cortical shavings from mature dormant canes. Molecular assays using radioactive or digoxigenin-labelled probes, RT-PCR, immunocapture RT-PCR, Real time PCR are currently the most used. RT-PCR is estimated to be four to sixfold more sensitive than ELISA. Three sets of degenerate primers were designed for each of the three Subgroups (A, B, and C) of the *Nepovirus* genus, based on the nucleotide sequence homology of the CP gene (RNA-2) and the untranslated region of RNA-1. These primers were able to detect simultaneously in RT-PCR all grapevine-infecting nepoviral species belonging to the same subgroup and to discriminate species of different subgroups. Indexing on *Vitis* indicators by grafting takes a lot of time and field or greenhouse space, but it is still regarded as necessary for confirming freedom from virus infection. Indexing on herbaceous hosts by mechanical inoculation requires climatized glasshouses and is less reliable than ELISA. Observation of symptoms in the field is useful as a first step in selection, but is not reliable. Detection of trabeculae can give information on the health of American rootstocks, but it is not a specific test. GFLV has been detected in small groups of viruliferous *X. index* (10 individuals) by ELISA and in single nematodes by RT-PCR and immunosorbent electron microscopy.

Control: Use of virus-tested scionwood and rootstock material in the framework of clean stock or certification programmes. Virus elimination is readily achieved from vegetating shoot tips by heat treatment (38-40°C for as little as four weeks), by *in vitro* meristem tip culture, or by somatic embryogenesis. Heat treatment was supposed to operate through a mechanism that increases viral degradation in the plant cell and slows down virus replication and movement towards the newly grown plant tissues. However, it has recently been found that RNA silencing, an antiviral immune-like defence sysem, is temperature-dependent and is significantly enhanced at higher temperatures, hence leading to increased degradation rates of viral RNA. In contaminated soils, the use of fumigants against nematode vectors gives only a temporary but economically valuable control of the disease. However, use of fumigants has been increasingly questioned for environmental reasons and is now virtually banned. Various *Trichoderma* species have been successfully used for the control of *Xiphinema index* in the laboratory. Also, some rhizobacteria isolated from grapevines protected the roots from damage caused by *X. index*, suggesting that they can be used in biological control programmes. The suitability of crop rotation or fallow before replanting new vineyards on soils that had hosted old infected plantings has been investigated with contradictory results. Earlier suggestions that a 3-year rotation could suffice for a dratical reduction of *X. index* populations were not supported by the finding that GFLV is still prsent in the vectors for up to four years in the apparent absence of host roots, and that soils infested by *X. index* need to be left fallow or grown for 6 to 10 years with plants other than vines and figs (*Ficus carica*), the latter being an excellent host of *X. index*. Work is under way in different laboratories to create GFLV-resistant rootstocks or cultivar through traditional breeding methods or genetic transformation technology which was developed for grapevines in the early 1990s. For transformation, a number of selectable marker genes toxic to non engineered vines are used. Mannose and xylose, which are desirable as they cause no harm to human health, are toxic to many plants but not to *V. vinifera.*

2. HISTORICAL REVIEW.

From the late 1800 to 1997, the ICVG Bibliographic Reports[(a)] have recorded more than 1,000 papers dealing with fanleaf. For a comprehensive review on early observations, research and hypotheses on fanleaf, as well as on the controversies about transmission by phylloxera, see the book by Galet (1977)[(b)].

1865 **Cazalis-Allut**: Description of grapevine degeneration in Frontignan (France).

1882 **Rathay**: Description of fanleaf disease from Austria (Zwiewipflereben).

1895 **Ruggeri**: Description of fanleaf disease from Italy (Roncet).

1896 **Cholin**: Description of fanleaf disease from Germany (Reisigkrankheit).

1902 **Baccarini**: First suggestion that fanleaf may be due to a virus.

1906 **Schiff-Giorgini**: Graft-transmission of fanleaf disease.

1912 **Pantanelli** : Fanleaf disease has a patchy distribution in the field.

1912 **Petri**: Association of trabeculae with fanleaf.

1917 **Pantanelli**: Fanleaf caused by contamination through the roots possibly due to heat-labile toxic substances.

1918 **Petri**: Disinfection of contaminated soil at 120°C or filtration of liquid leached from contaminated soil

(a) See references in "Introduction".

(b) Galet P., 1977. Les maladies et les parasites de la vigne. Tome 1: Les maladies dues à des végétaux (champignons, bactéries, viroses et phanérogames). Imprimerie du Paysan du Midi", Montpellier, France, 871 pp.

through porcelain filter prevents infection through the roots of grapevine. Hypothesis that fanleaf is a fungal disease.

1929 **Petri:** Grapevine "arricciamento" (fanleaf) has a viral origin.

1931 **Arnaud and Arnaud**: Hypothesis of a viral origin for grapevine court-noué (fanleaf).

1937 **Arnaud**: Court-noué is considered as a soil-borne virus disease. Hypothesis about a possible role of phylloxera as a vector.

1937 **Branas** *et al.*: Hypothesis that court-noué (fanleaf) is caused by a virus transmitted by phylloxera. No direct proof of transmission by this aphid, but only circumstantial evidence.

1946 **Branas** *et al.*: Experiments on the capacity of phylloxera to transmit fanleaf. Healthy rooted cuttings or seedling of Rupestris du Lot were contaminated:

1. With roots of fanleaf-infected grapevines with phylloxera feeding on them;
2. With individual phylloxera (radicicolous or gallicolous) fed on infected vines;
3. With soil containing phylloxera.

No conclusive results were obtained.

1910 **Pantanelli**: Fanleaf disease can be transmitted through the soil.

1950a, b **Hewitt**: Fanleaf and yellow mosaic recorded from California.

1954 **Hewitt**: Review on grapevine virus and virus-like diseases found in California.

1958 **Bovey**: Review on grapevine virus and virus-like diseases. First experiments using heat treatment for eliminating fanleaf. Heating whole plants in a thermostatic chamber at 37°C for several weeks provides a temporary elimination of symptoms on the new growth but no lasting cure.

1958 **Vuittenez**: Fumigation of fanleaf-contaminated soil with nematicides prevents infection of healthy grapevines replanted immediately, whereas insecticide treatment has no effect.

1958 **Hewitt** *et al.*: Fanleaf virus is transmitted by the nematode *Xiphinema index.*

1960 **Cadman** *et al.*: Transmission of fanleaf virus from grapevine to herbaceous hosts by mechanical inoculation and preliminary characterization of the virus. Serological relationship with ArMV reported.

1960a **Vuittenez**: New observations on the effects of soil fumigants on fanleaf in contaminated soils.

1960b **Vuittenez**: Mechanical transmission of fanleaf virus to *Chenopodium quinoa* and *C. amaranticolor* is confirmed.

1961 **Brückbauer and Rüdel**: The virus (or viruses) of Reisigkrankheit (GFLV and/or other nepoviruses) are seed-transmitted in some herbaceous indicator plants. Discussion on the possible role of weeds in the epidemiology of the disease.

1961 **Gifford and Hewitt**: Use of heat therapy and *in vitro* shoot tip culture to eliminate fanleaf virus from infected grapevines.

1962 **Hewitt** *et al.*: Investigations on grapevine virus diseases in California. Description of the chip-budding method for indexing. Control of *X. index* by soil fumigation.

1962 **Goheen and Hewitt**: Description of vein banding as a GFLV-induced disease.

1963 **Dias**: Host range and properties of fanleaf and yellow mosaic viruses.

1963 **Dias and Harrison**: Relationships between the viruses causing fanleaf, yellow mosaic and ArMV.

1963a, b **Martelli and Hewitt:** Comparative studies show that Californian and Italian GFLV strains are the same. Reproduction of fanleaf symptoms in mechanically inoculated grapevine seedlings.

1963 **Martelli and Raski**: Consistent association of *Xiphinema index* with fig (*Ficus carica)* and to lesser extent with mulberry (*Morus* spp.) in Apulia (southern Italy).

1964 **Taylor and Hewitt**: Description and characterization of Australian isolates of GFLV. Reproduction of fanleaf symptoms in mechanically inoculated grapevine seedlings is confirmed.

1964 **Galzy**: Heat treatment of grapevine plantlets grown aseptically *in vitro.*

1965 **Goheen** *et al.*: Description of the Davis method of heat therapy of grapevines. Potted plants to be cured are grown at 38°C for several weeks, shoot tips are cut and rooted under mist in a greenhouse.

1965 **Graniti and Russo**: A light microscope and cytochemical study of endocellular cordons.

1967 **Bercks**: Research on the use of three serological methods for detecting plant viruses, including GFLV: bentonite flocculation, latex, and barium sulfate.

1968 **Das and Raski**: Studies on the relationships of GFLV with its vector *X. index.*

1968 **Hewitt**: First comprehensive review on virus diseases of the grapevine.

1968 **Boubals and Dalmasso**: Experiments on soil disinfection against *X. index* in France. Dichloropropane-dichloropropene (DD) at 1000 l/ha gave satisfactory results, and no reinfestation by *X. index* occurred during the 6-year period of observation.

Yield was increased by 400% in comparison with that of untreated controls.

1969 **Bercks and Querfurth**: Use of latex-test for detecting GFLV and other nepoviruses in grapevine tissue extracts in Germany.

1969 **Gerola** *et al.*: Detection of GFLV particles in thin-sectioned grapevine root tissues.

1970 **Cohn** *et al.*: Transmission of GFLV by *Xiphinema italiae* in Israel.

1970 **Hewitt** *et al.*: Description of GFLV in the CMI/AAB Descriptions of Plant Viruses.

1970 **Taylor and Robertson**: GFLV and ArMV are retained as a monolayer of particles adsorbed onto the cuticle lining the lumina of odontophore, anterior oesophagus and oesophageal bulb of their nematode vectors. During nematode moult, this lining is shed and ingested in the intestine.

1970 **Vuittenez**: Review paper on grapevine fanleaf.

1970 **Dias**: Review paper on grapevine yellow mosaic.

1970 **Taylor**: Review paper on grapevine vein banding.

1971 **Bercks**: Serological detection of grapevine viruses in West Germany.

1971 **Raski** *et al.*: Control of fanleaf by soil fumigation with 1,3 dichloropropene or methyl bromide.

1972 **Raski and Schmitt**: Progress in the control of the fanleaf-nematode complex by soil disinfection with 1,3-dichloropropene or methyl bromide. Vineyards replanted in contaminated but treated soils remained healthy for at least 5 years.

1972 **Mur** *et al.*: Heat therapy of grape plantlets grown *in vitro* causes changes in some characteristics of the variety.

1973 **Raski** *et al.*: GFLV particles observed in the lumen of the oesophagus of *X. index*.

1973 **Goheen and Luhn**: New method of heat therapy. A dormant bud of the variety to be cured is grafted onto a healthy potted rootstock. After bud take, the plant is placed in a heat cabinet for treatment.

1973a **Hévin** *et al.*: Use of green grafting as a quick and secure method for graft-indexing.

1973b **Hévin** *et al.*: GFLV and marbrure (fleck) are not transmitted through the seeds of grapevine.

1974 **Van Velsen and Niejalke**: Green budding for indexing grapevine with the indicator cvs. St. George, Mission or LN 33.

1974 **Alfaro and Goheen**: The different strains of fanleaf virus (fanleaf *sensu stricto*, yellow mosaic and vein banding) are transmitted in the same way by *X. index*. The acquisition time threshold is less than 5 min. Indexing by budding on *V. rupestris* is more accurate than mechanical transmission to *C. quinoa*.

1975 **Martelli and Piro**: Evidence from a herbarium of dried specimens collected between 1880 and 1886 that fanleaf and yellow mosaic occurred in field-grown grapevine in Sicily in the second half of the 19th century.

1976 **Quacquarelli** *et al.*: Detailed physico-chemical characterization of GFLV.

1976 **Uyemoto** *et al.*: Comparison of indexing by mechanical inoculation to *Chenopodium quinoa* and by graft-transmission to *V. rupestris* St. George for detecting GFLV. Both methods give satisfactory and similar results.

1977 **Bass and Vuittenez**: Thermotherapy was improved by growing shoot apices of heat- treated vines aseptically on nutritive media or by grafting them on aseptic grape seedlings *in vitro*.

1978 **Vovlas** *et al.*: *Xiphinema index* induces the same type of anatomical alteration in the roots of *Vitis rupestris* and a *Vitis vinifera* × *Muscadinia rotundifolia* hybrid.

1979 **Querfurth and Paul**: Protein A-coated latex-linked antiserum (PALLAS) method for detecting GFLV and other viruses. The sensitivity of the latex test is increased, especially with low titre antisera.

1979 **Walter** *et al.*: Comparison between PALLAS test and ELISA for detecting GFLV in France. Both tests are more sensitive than mechanical inoculation on *C. quinoa*. PALLAS is quicker and cheaper than ELISA, but ELISA is more sensitive.

1979 **Kalasian** *et al.*: GFLV particles are arrayed in long parallel rows in thin-sectioned mesophyll cells of infected grapevines.

1980 **Vuittenez**: Review on serological methods of detection and identification of grapevine viruses.

1980 **Rüdel**: Discussion on the possible role of *X. vuittenezi*, a very common species in vineyards of Rheinhessen and Palatinate, as vector of GFLV. Transmission trials gave a few positive results. Even in the cases where the virus was transmitted, the possibility that a few *X. index* larvae were present in the *X. vuittenezi* population used for the experiments could not be entirely ruled out. That *X. vuittenezi* might be a vector of GFLV is therefore uncertain.

1980 **Brown and Roberts**: Detection of fanleaf virus in its vector *X. index* by ISEM.

1980 **Bovey** *et al.*: Detection of fanleaf virus in grapevine tissues by ELISA and ISEM at different periods of the year. Efficiency of both methods is compared.

1980 **Russo** *et al.*: Detection of fanleaf virus and other sap-transmissible viruses in grapevine tissues by ISEM.

1981 **Raski** *et al.*: Experiments with systemic nematicides for controlling *X. index.*

1981 **Hafez** *et al.*: Use of systemic nematicides for the control of *X. index.*

1981 **Lear** *et al.*: Study on the effectiveness of soil fumigation for the control of *X. index* and fanleaf in grapevines. Methyl bromide and 1,3-dichloropropene failed to eradicate either nematodes or fanleaf virus from the soil but reduced the incidence of the disease to acceptable levels. Carbon disulfide gave less satisfactory results.

1981 **Bouquet**: *M. rotundifolia* becomes infected by GFLV when the virus is transmitted by grafting but resists infection when transmission is by *X. index* feeding.

1983a **Bouquet**: *Muscadinia rotundifolia* is resistant to fanleaf virus transmission by *X. index*, although it is not resistant to the virus itself.

1983b **Bouquet**: Serological detection of GFLV in its vector *X. index* by ELISA.

1983 **Raski** *et al.*: Soil fumigation with 1,3-dichloropropene (1,3-D) or methyl bromide applied 75-90 cm deep with 90 cm spacing for 1,3-D (1400 l/ha) and 50-75 cm deep with 165 cm spacing for methyl bromide (448 kg/ha) gave a good control of *X. index*, in California. The use of methyl bromide requires a continuous cover with polyethylene sheeting for some time after the treatment.

1983 **Krake and Woodham**: Possibility that the agent of yellow speckle is involved together with GFLV in the aetiology of vein banding.

1983 **Morris-Krsinich** *et al.*: *In vitro* translation of genomic RNAs of GFLV yields two large polyproteins (220 KDa and 125 KDa) which are subsequently processed by proteolytic cleavage to form mature structural and non structural proteins. RNA-2 contains the cistron coding for the viral coat protein.

1985 **Walker** *et al.*: Identification of several *Vitis* species and interspecific hybrids resistant to fanleaf virus. These are promising sources of germplasm for obtaining resistant rootstocks. A Middle Eastern *V. vinifera* accession represents an excellent example of host plant resistance to GFLV.

1985 **Savino** *et al.*: Identification of a natural serological variant of GFLV from Tunisia.

1986 **Huss** *et al.*: Comparison of polyclonal and monoclonal antibodies for detecting fanleaf virus with ELISA in various grapevine tissues, especially in wood shavings of dormant canes during winter.

1986 **Monette**: Heat therapy of GFLV- and ArMV-infected grapevines with alternating temperatures. Forty days of treatment, with temperatures of 39°C for 6 h followed by 22°C for 18 h eliminated both viruses from the developing shoot tips (2 mm) of *in vitro*-grown plantlets.

1987 **Huss** *et al.*: Production and use of monoclonal antibodies to GFLV.

1987 **Walter and Etienne**: Detection of GFLV in wood shavings of dormant canes.

1987 **Rüdel**: Review on the most important virus diseases of grapevines in West Germany. GFLV, RpRSV and ArMV are common, the latter being especially damaging on cv. Kerner. Effect on yield and economic importance. Treatments with soil fumigants are no longer permitted in Germany.

1988 **Raski and Goheen**: Comparison of 1,3-dichloropropene and methyl bromide for controlling *X. index* and GFLV. No eradication was obtained, however treated vines yielded more for over 4 years. Previous experience showed that 1,3-dichloropropene or methyl bromide fumigation following one year fallow period can give a satisfactory control of the disease for at least 12-15 years.

1988 **Rüdel**: Severe restrictions set on the use of soil fumigants in West Germany for environmental reasons make control of "Reisigkrankheit" very difficult. Long term fallow (about 5 years), cultivation of non-host plants and organic soil amendments are recommended. The selection of resistant cultivars and rootstocks is considered of primary importance.

1988 **Pinck** *et al.*: Identification of a satellite RNA of GFLV.

1989 **Catalano** *et al.*: Evidence of a differential efficiency of GFLV transmission by *Xiphinema index* populations from different geographical origins.

1989 **Walker** *et al.*: Two rootstock selections derived from crossings *V. vinifera* x *V. rotundifolia* showed good resistance to GFLV in California.

1989 **Fuchs** *et al.*: Determination of the nucleotide sequence of the satellite RNA (RNA-3) of GFLV. RNA-3 encodes a non structural protein, and has strong homologies with the satellite RNA associated with ArMV.

1989 **Altmayer**: Elimination of GFLV, ArMV, RRV, SLRV, TBRV and leafroll from infected grapevines by *in vitro* meristem tip culture.

1989 **Walter** *et al.*: Improvement in the serological detection of GFLV and ArMV viruses using monoclonal antibodies.

1990 **Walter** *et al.:* Use of green grafting technique for sensitive and quick GFLV detection under greenhouse conditions.

1990 **Lázár** *et al.*: Detection of GFLV in grapevine seeds and seedlings by ELISA.

1990 **Serghini** *et al.*: Determination of the complete sequence of GFLV RNA-2.

1990 **Martelli and Taylor**: Review article on nematode-transmitted viruses.

1990 **Walker and Meredith**: Identification of two accessions of *Vitis vinifera* resistant to GFLV. Resistance is controlled by two unliked recessive genes.

1990 **Mullins** *et al.*: First report of successful Agrobacterium-mediated transformation of grapevines.

1991 **Walter** *et al.*: Study of interactions between GFLV and ArMV isolates grown in *C. quinoa* and transmitted by heterografting to Vialla and Kober 5BB rootstocks. Mild and severe strains were discriminated on the basis of field performance of infected *Vitis*. Mild strains were shown to confer protection towards severe challenging strains in *Chenopodium* and grapevine.

1991 **Etienne** *et al.*: Possibility of detecting several nepoviruses or serotypes of nepoviruses in grapevine leaves or wood shavings in a single DAS-ELISA test using a mixture of different polyclonal antisera.

1991 **Catalano** *et al.*: Detection of GFLV in the vector *Xiphinema index* by ELISA. Viruliferous nematodes were crushed in standard extraction buffer and tested in batches of 1-50 by means of DAS-ELISA. Reliable results were obtained with samples of 20-50 nematodes. Positive, but less consistent results were obtained with 1-10 nematodes.

1991a **Fuchs** *et al.*: Development of cDNA probes to GFLV genomic and satellite RNAs and their use for virus detection directly in grapevine extracts.

1991b **Fuchs** *et al.*: Co-inoculation of *C. quinoa* with biologically active transcripts of GFLV F-13 satellite RNA and GFLV strains devoid of satellite, delays symptom expression by 1-2 days and adversely affects virus replication. Satellite RNA appears to have a modulating effect on virus pathogenicity.

1991 **Staudt**: Study of the spread of GFLV in several *Vitis* species, hybrids and breeding stocks after infection of the roots by means of viruliferous *X. index*.

1991 **Ritzenthaler** *et al.*: Genomic RNA-1 of GFLV is completely sequenced and its genetic organization determined.

1992 **Staudt and Weischer:** *Vitis rotundifolia* and *Vitis munsoniana* resist infection by GFLV transmitted by *X. index.*

1992 **Goussard and Wiid**: First application of somatic embryogenesis for sanitation of grapevines. GFLV is eliminated from somatic embryos obtained from tissue cultures grown at 35°C.

1992a, b **Hans** *et al.*: Production of GFLV satellite RNA transcripts, identification of their replication determinants and evidence of replication in *Chenopodium quinoa* protoplasts.

1993 **Martelli** *et al.*: European virologists propose a certification scheme for grapevine.

1993 **Gemmrich** *et al:* Development and use digoxigenin-labelled cDNA probes for the molecular detection of GFLV.

1993 **Nolasco and De Sequeira**: Design and use of primers for specific amplification of GFLV sequences by IC-PCR.

1993 **Nolasco and De Sequeira**: Molecular variability in the genome of GFLV isolates coming from the same vineyard assessed by IC-PCR combined with RFLP and SSCP analysis. GFLV is a quasispecies occurring in the field as a series of minor molecular variants.

1993 **Viry** *et al.*: Production of biologically active transcripts from cloned cDNA of genomic RNAs of GFLV.

1993 **Spielmann** *et al.*: Use of modified GFLV coat protein genes for transformation of different *Nicotiana* species for inducing resistance.

1993 **Walter** *et al.*: In naturally GFLV-infected vineyards the hypovirulent ArMV A1 isolate induces delayed infection by GFLV.

1993 **Saldarelli** *et al.*: GFLV satellite RNA detected in 5 of 34 virus isolates from different geographical locations.

1993 **Esmenjaud** *et al.*: Detection of GFLV in *X. index* by biotin-avidin ELISA.

1993 **Margis** *et al.*: *In vitro* cleavage products of the RNA-2-encoded polyprotein of GFLV disclose the genome oganization of viral RNA-2.

1994 **Bardonnet** *et al.*: Evidence that transgenic tobacco plants expressing the coat protein of GFLV are protected from GFLV infection.

1994 **Horvath** *et al.*: GFLV isolated in Hungary from naturally infected symptomatic plants of *Aristolochia clematis* and *Lagenaria siceraria turbinata.* This represents the first substantiated record of a natural GFLV infection in hosts other than *Vitis.*

1994 **Esmenjaud** *et al.*: Detection of GFLV in single nematodes by RT-PCR.

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INFECTIOUS DEGENERATION (EUROPEAN AND MEDITERRANEAN NEPOVIRUSES)

Besides GFLV, several other nepoviruses can infect grapevine in Europe, the Mediterranean and Middle East, causing diseases whose symptoms are similar to, or indistinguishable from those of fanleaf. Several of these viruses have distorting and chromogenic strains and may occur in mixed infections with GFLV. All have polyhedral particles about 30 nm in diameter and a positive sense, single-stranded RNA genome occurring as two functional species (RNA-1 and RNA-2), which are separately encapsidated (Harrison and Murant, 1996). Many are transmitted by longidorid nematodes (Rüdel, 1992; Taylor and Brown, 1997). Serological (ELISA, ISEM) and molecular assays (hybridization, RT-PCR) are routinely used for their detection in grapevine tissues (primarily cortical scrapings from dormant canes) (Rowhani *et al*., 2005) Mechanical transmission to herbaceous hosts or indexing on *Vitis* indicators can also be used. These viruses are readily eliminated by heat therapy or *in vitro* meristem tip culture. Their detrimental effects to grapevine culture and products have been summarized by Walter and Martelli (1996).

Nepoviruses, which were originally included in the Nepovirus group (Harrison and Murant, 1977), a non-taxonomic clustering, were then classified in the genus *Nepovirus*, family *Comoviridae* (Goldbach *et al*., 1995) and lately in the family *Secoviridae*. The genus *Nepovirus* is subdivided into subgroups based on physico-chemical properties of its members, i.e. subgroup A typified by *Tobacco ringspot virus* (TRSV); subgroup B, typified by *Tomato black ring virus* (TBRV); subgroup C, typified by *Tomato ringspot virus* (ToRSV) (Martelli *et al*., 1978; Murant 1981, Le Gall *et al*., 2005). *Strawberry latent ringspot virus* (SLRSV), a nematode-borne virus originally classified as a tentative species in the genus *Nepovirus*, then in the newly established genus *Sadwavirus* (Le Gall *et al*., 2005), is currently placed the family *Secoviridae* as an unassigned species (Sanfaçon *et al*., 2011).

Extensive reviews of the biological, epidemiological, physico-chemical, and molecular characteristics of nepoviruses (Martelli and Taylor, 1990; Harrison and Murant, 1996; Taylor and Brown, 1997) and their satellite RNAs (Mayo *et al*., 2000) are available.

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GENUS *NEPOVIRUS*

ARABIS MOSAIC VIRUS (ArMV)

1. DESCRIPTION

ArMV, a typical nepovirus belonging in subgroup A of the genus, is serologically related to GFLV. Its particles are about 30 nm in diameter, have a angular outline, and sediment as three components (T, M, and B). Component T is made up of empy protein shells, whereas components M and B contain RNA. Coat protein has a single type of subunits with M_r 54×10^3. The genome is a positive sense ssRNA, consisting of two separately encapsidated molecules with Mol. wt 2.2×10^6 (RNA-1) and $1.95\text{-}2.1\times10^6$ (RNA-2), accounting for 27% (component M) and 41% (component B) of the particle weight. Two types of RNA-2 molecules have been found which differ slightly in size (3852 and 3711 nt) but contain a single ORF encoding polypeptides with M_r of 119 and 124 kDa, respectively. The virus supports the replication of two types of satellite RNAs, linear with Mol. wt of 0.4×10^6 and a size of 1104 nt and circular about 350 nt in size. ArMV occurs often in mixed infections with GFLV in certain areas of France and Italy, and with other nepoviruses in the Reisigkrankheit complex of western Germany. This virus has also been found in grapevine in Switzerland, Spain, Italy, Bulgaria, Yugoslavia, Hungary, Romania, Turkey, Iran, Israel, Canada, USA (California, New York), and Japan. Natural recombinants between ArMV and GFLV are frequently found in nature. ArMV can infect many woody and herbaceous plants and is transmitted to grapevine by the nematode *Xiphinema diversicaudatum* but not by *X. index*, the vector of GFLV. In Germany, losses up to 50% have been recorded, and, always in Germany the severe dieback disease of the cv. Kerner appears to be caused by ArMV infection. In other *V. vinifera* varieties, symptoms are of the fanleaf type. Cross-protection between ArMV and GFLV has been reported. Transgenic plants expressing the coat protein gene of the virus have been produced.

2. HISTORICAL REVIEW

1963 **Panjan and Saric**: ArMV detected in grapevine in Yugoslavia.

1964 **Gerola** *et al.*: Ultrastructure of ArMV infections in plant tissues.

1968 **Martelli and Lehoczky**: Detection of ArMV in grapevine in Hungary.

1970 **Stellmach**: Review paper on ArMV in grapevine.

1970 **Murant**: ArMV description in the CMI/AAB Descriptions of Plant Viruses series.

1972 **Dalmasso** *et al.*: *Xiphinema diversicaudatum* can transmit ArMV to grapevine.

1976 **Brückbauer and Rüdel**: Symptoms of atypical Reisigkrankheit in the vineyard are associated with ArMV in West Germany.

1977 **Bercks** *et al.*: ArMV, SLRSV and TBRV found in grapevines with atypical Reisigkrankheit in West Germany.

1978 **Rüdel**: Transmission of ArMV to grape seedlings by *Xiphinema diversicaudatum.*

1978 **Jankulova and Kaitasova**: ArMV found in grapevine in Bulgaria.

1979 **Vuittenez** *et al.*: Interactions between nepoviruses in grapevine and herbaceous hosts.

1979 **Quacquarelli** *et al.*: Physico-chemical properties of GFLV, ArMV, TBRV, AILV and GCMV.

1980 **Kobayashi** *et al.*: ArMV detected in Japan in grapevines imported from Europe.

1980 **Russo** *et al.*: Detection of ArMV by ISEM.

1980 **Tanne**: Detection of GFLV, ArMV and TBRV by ELISA in Israel.

1982 **Belli** *et al.*: Isolation of ArMV from grapevine in Italy.

1982 **Brückbauer**: Possibility of distinguishing GFLV, ArMV, RRV, SLRV and TBRV.

1984 **Belli** *et al.*: Properties of a strain of ArMV isolated from grapevine in Italy.

1985 **Rüdel**: In the Palatinate (West Germany) ArMV is transmitted by *Xiphinema diversicaudatum* and occurs often in mixed infections with GFLV in grapevine. Yield losses may reach 77% in cv. Faber.

1986 **Stellmach and Berres**: The susceptibility of cv. Kerner to ArMV seems to be limited in time. When a healthy scion is grafted onto an infected rootstock, the virus is recovered from the scion only during the first year, whereas the rootstock remains infected. Hypothesis of a graft incompatibility when the rootstock is infected with ArMV.

1987 **Stellmach**: Kerner disease is probably caused by ArMV.

1988 **Kaper** *et al.*: Nucleotide sequence of a small circular satelllite RNA associted with ArMV.

1989 **Steinkellner** *et al.*: Use of cDNA probes for ArMV detection. Molecular assays are as good as ELISA for routine testing.

1989 **Becker** *et al.:* Association of ArMV-infected rootstocks with Kerner disease in West Germany. The virus cannot be recovered from leaves or buds of the Kerner scions, whereas other nepoviruses, such as RpRSV or GFLV are found in rootstocks and scions. Study of histological changes at the graft union level.

1989 **Eppler** *et al.*: ArMV in Romania.

1989 **Huss** *et al.*: Cross-protection experiments in *Chenopodium quinoa* between ArMV and GFLV.

1990 **Gugerli** *et al.*: ArMV in Switzerland.

1990 **Lázár** *et al.*: ArMV is not seed-transmitted in grapevines.

1990 **Liu** *et al.*: Nucleotide sequence of the ArMV satellite RNA.

1991 **Liu** *et al.*: The presence of ArMV satellite RNA can attenuate symptoms in certain hosts.

1991 **Bertioli** *et al.*: Transgenic *Nicotiana* plants transformed with the coat protein of ArMV produce empty viral shells.

1992 **Ipach** *et al.*: Detection of ArMV by PCR in herbaceous hosts and grapevines.

1992 **Steinkellner** *et al.*: Comparison of coat proteins of ArMV and other nepoviruses.

1993 **Walter** *et al.:* A hypovirulent ArMV isolate delays GFLV infection in grapevines under field conditions.

1993 **Steinkellner** *et al.*: *Nicotiana* plants engineered with ArMV coat protein gene show different degrees of tolerance to the virus.

1994 **Flak and Gangl**: ArMV in Austria.

1995 **Loudes** *et al.*: Evidence that ArMV has two RNA-2 molecules and determination of the complete nucleotide sequence of both RNAs.

1995 **Etscheid** *et al.*: Properties of ArMV small satellite RNA.

1995 **Marc-Martin** *et al.*: Transformation of grapevines with the coat protein gene of ArMV.

1996 **MacKenzie** *et al.*: Survey for the presence of ArMV in Canadian vineyards.

1996 **Lahogue and Boulard**: Search for genes of resistance in grapevines. Of 407 accessions of European, American, and Asian *Vitis* species inoculated by green grafting with an ArMV source, 42 were apparently resistant.

1998 **Akbas and Erdiller:** ArMV in Turkey.

2000 **Goelles** *et al.*: Production of transgenic grapevines expressing ArMV coat protein gene.

2000 **Spielmann** *et al.: N. benthamiana* transformed with the CP gene of ArMV resists infection. Virus-like ArMV particles are formed in transgenic plants.

2001 **Wetzel** *et al.*: Complete RNA-2 sequence of German grapevine isolates of ArMV and GFLV.

2002a **Wetzel** *et al.*: Simultaneous detection and discrimination of GFLV and ArMV with a single pair of primers.

2002b **Wetzel** *et al.*: ArMV isolates from nine distinct hosts, grapevine included, are classified into four groups based on the size of protein $2A^{HP}$.

2003 **Fuchs**: Review on transgenic resistance of grapevines to pathogens.

2004 **Pourrahim** *et al.*: ArMV identified in Iranian grapevines.

2004 **Wetzel** *et al.*: Nucleotide sequence of the RNA-1 of a grapevine isolate of ArMV.

2008 **Wetzel** *et al.*: Identification of the proteinase cleavage sites in the RNA-1-encoded polyprotein of ArMV.

2009 **Borroto** *et al.*: Elimination of ArMV by somatic embryogenesis.

2010 **Abelleira** *et al.*: First record of ArMV from Spain.

2012 **Spilmont** *et al.*: Efficient elimination of ArMV (81%) by micrografting on cv. Vialla seedlings.

2013 **Celebi-Toprak** *et al.*: ArMV in New York State.

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ARTICHOKE ITALIAN LATENT VIRUS (AILV)

1. DESCRIPTION

Artichoke Italian latent virus (AILV), a member of subgroup B of the genus *Nepovirus* was isolated in Bulgaria from vines with fanleaf-like symptoms. AILV has isometric particles with angular outline, sedimenting as three components: T (empty shells), M (particles contaning a molecule of RNA-2 with Mol. wt of 1.5×10^6 daltons accounting for 34% of the particle weight) and B (particles containing a molecule of RNA-1 with Mol. wt of 2.4×10^6 daltons, accounting for 41% of the particle weight). Coat protein is made up of a single type of subunits with M_r 54×10^3. AILV is transmitted by the Dorylaimoid nematode *Longidorus apulus* in vegetable crops but no field transmission to grapevines has been recorded. The virus has limited distribution and economic importance.

2. HISTORICAL REVIEW

1976 **Jankulova** *et al.*: AILV isolated in southern Bulgaria in 1976 from a grapevine with fanleaf-like symptoms. Properties of the virus, cultured in *Chenopodium quinoa.* determined and positive serological reaction with an antiserum to an Italian strain of AILV ascertained.

1976 **Savino** *et al.*: Comparison of a Bulgarian grapevine isolate of AILV with an Italian isolate from artichoke and two Bulgarian isolates from sowthistle and gladiolus.

1977 **Martelli** *et al.*: AILV description in the CMI/AAB Descriptions of Plant Viruses series.

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CHERRY LEAFROLL VIRUS (CLRV)

1. DESCRIPTION

Cherry leafroll virus (CLRV) is a cosmopolitan virus. In Chile it was recovered from vines with fanleaf-like symptoms and in Germany from vines with yellow mosaic-like symptoms. It occurs also in Poland. Although CLRV is a definitive nepovirus species classified in subgroup C of the genus *Nepovirus* it differs from most of the other members in the genus being transmitted by pollen rather than nematodes. The vector to grapevine, if any, is unknown. CLRV occurs in nature as multiple strains but is not serologically related to any of the known nepoviruses. Virus particles are isometric, about 30 nm in diameter have angular outline and sediment as three components (T, M, and B). Their coat protein consists of a single type of subunits with M_r of about 54 kDa. The genome is a bipartite, positive sense, single-stranded RNA which has been totally sequenced. Genomic RNA consists of two separately encapsidated functional molecules. RNA-1 accounts for 46% of the particle weight, has a mol. wt of 2.8×10^6, is 7,918 nt in size and encapsidates a polyprotein 2112 aa long, 236 kDa in size. RNA-2 accounts for 41% of the particle weight, has a mol wt of 2.3×10^6, is 6,360 nt in size and encapsidates a polyprotein 1589 aa long, 175 kDa in size. In grapevines CLRV is readily detected by DAS-ELISA. The best woody indicator for the German isolate is reported to be Pinot noir.

2. HISTORICAL REVIEW

1985 **Jones:** Description of *Cherry leafroll virus* in the AAB Descriptions of Plant Viruses series.

1993 **Scott** *et al.*: Partial nucleotide sequence of CLRV RNA-.

2001 **Herrera and Madariaga**: First record of CLRV from Chile. Field infection is estimated to be 0.2%.

2003 **Ipach** *et al.*: Isolation of CLRV from German vines showing yellow mosaic-like symptoms and reduced crop.

2012 **von Bargen** *et al.*: Complete sequence of both genomic RNAs of CLRV.

2012 **Komorowska** *et al.*: CLRV in Poland.

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GRAPEVINE ANATOLIAN RINGSPOT VIRUS (GARSV)

1. DESCRIPTION

GARSV was isolated from Turkish grapevines with mild fanleaf-like symptoms. The virus belongs in subgroup B of the genus *Nepovirus* but is not serologically related to any of the known grapevine nepoviruses. Virus particles are isometric *c.* 30 nm in diameter and sediment as three centrifugal components. RNA-1 has a mol. wt of 2.2×10^6 Da, a size of 7,288 nt, encoding a polypeptide of 2,243 aa with a predicted M_r of 259 kDa. RNA-2 has a mol. wt of 1.4×10^6 Da and a size of 4,607 nt. Coat protein subunits have a M_r 56×10^3 Da. The virus is phylogenetically related to *Tomato black ring virus* (TBRV) and *Grapevine chrome mosaic virus* (GCMV).The suggestion has been put forward that a recombination between GARSV and TBRV may have given rise to GCMV. GARSV can be readily detected by ELISA and PCR using primers designed on the coat protein sequence. The virus has no recognized vector, is not seed-borne and occurs in south-eastern Turkey and Iran. The scattered distribution of infected vines in the field suggests that the virus is spread primarily by infected propagative material.

2. HISTORICAL REVIEW

2002 **Cigsar** *et al.***:** First isolation by mechanical transmission of an unknown nepovirus from cv. Kizlar tahtasi showing mild fanleaf-like symptoms.

2003 **Gokalp** *et al.*: Description and thorough characterization of GARSV identified as a new species in the subgroup B of the genus *Nepovirus.*

2005 **Abou Ghanem-Sabanadzovic** *et al.*: Complete nucleotide sequence of GARSV RNA-2.

2012 **Hajizadeh** *et al.*: GARSV in Iran.

2012 **Digiaro** *et al.*: Complete nucleotide sequence of GARSV RNA-1.

2014 **Digiaro** *et al.*: GARSV and *Tomato black ring virus* recognized as putative parents of of the interspecies recombinant *Grapevine chrome mosaic virus.* The recombination event is at the movement protein ($2B^{MP}$) level.

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GRAPEVINE BULGARIAN LATENT VIRUS (GBLV)

1. DESCRIPTION

GBLV owes it name to the fact that it was found for the first time in Bulgaria in 1971, where it is widespread

and infects latently several grapevine varieties growing in widely separared areas. GBLV is a typical nepovirus belonging in subgroup C of this genus but its vector is unknown. The virus occurs as different closely related but serologically distinguishable strains. Virus particles are about 30 nm in diameter and sediment as three components (T, B1, and B2). Component T is made up of empty protein shells, whereas components B_1 and B_2 contain RNA. The coat protein has a single type of subunits with M_r 54×10^3. The genome is a positive sense ssRNA, consisting of two separately encapsidated molecules with mol. wt of 2.2×10^6 (RNA-1) and $1.95\text{-}2.1\times10^6$ (RNA-2), accounting for 39% (component B1) and 42% (component B2) of the particle weight. RNA-1 is 7,452 nt in length, contains a single ORF of 6,285 nt expressing a polypeptide 2.095 aa in size with a predicted M_r of *ca.* 234 kDa. RNA-2 is 5,821 nt in length, contains a single ORF of 4,500 nt expressing a polypeptide 1,500 aa in size with a predicted M_r of *ca.*167 kDa. The virus supports the replication of a satellite RNA with mol. wt 0.5×10^6 (less than 1800 nt). A strain of this virus had been found previously in Portugal and described as virus CM112. GBLV has also been recorded from Hungary and Yugoslavia. By contrast, a virus serologically related to GBLV found in Concord grapes in New York State vineyards is a strain of *Blueberry leaf mottle virus* (BLMoV), a North American nepovirus species related to, but different from GBLV. Two isolates of GBLV have been transmitted by mechanical inoculation to seedlings and rooted cuttings of several grapevine cultivars without inducing symptoms. The economic importance of the virus is minor.

2. HISTORICAL REVIEW

1972 **Ferreira and De Sequeira:** Description and preliminary characterization of an unidentified virus denoted CM112, isolated in 1970 in Portugal from symptomless vines.

1972 **De Mendonça** *et al.*: Isolation of virus CM112 from *in vitro* cultures of grapevine tissues.

1977 **Martelli** *et al.*: Description of GBLV. Biological, physico-chemical and serological characterization of the virus and assignment to the Nepovirus group (now genus *Nepovirus*). The virus can be detected directly in grapevine leaf extracts by immunodiffusion in agar plates.

1977 **Uyemoto** *et al.*: A virus serologically related to GBLV isolated from *Vitis labrusca* cv. Concord in New York State.

1978 **Martelli** *et al.*: GBLV description in the CMI/AAB Descriptions of Plant Viruses series.

1979 **Martelli** *et al.***:** A comparative study of three GBLV isolates from Bulgaria shows that they are closely related but serolgically distiguishable and that can infect seedlings and rooted cuttings of different grapevine cultivars without inducing symptoms.

1980 **Dimitrijevic**: GBLV found in Yugoslavia.

1980 **De Mendonça** *et al.*: Detection of virus CM112 in grapevine leaf extracts by ISEM.

1980 **Martelli** *et al.*: Ultrastructural study of GBLV infections in grapevine and *C. quinoa.*

1980 **Russo** *et al.*: Detection of GBLV in grapevine leaf extracts by ISEM.

1981 **Ramsdell and Stace-Smith**: The New York isolate of GBLV is a strain of BLMoV.

1981 **Pocsai**: Occurence of GBLV in Hungary.

1982 **Varennes and De Sequeira**: First application of ELISA for the detection of virus CM112.

1983 **Gallitelli** *et al.*: A comparative study of Bulgarian GBLV isolates and the Portuguese virus CM112 establishes that CM112 is a serologically close but distinguishable strain of GBLV. The Portuguese strain supports the replication of a satellite RNA.

1985 **De Sequeira and Vasconcelos-Costa**: Use of an immunoradiometric assay for the titration of the Portuguese strain of GBLV.

1992 **Krastanova** *et al.*: Improvement of ELISA protocol for GBLV detection the whole year round.

2011 **Elbeaino** *et al.:* Complete nucleotide sequence of the GBLV genome.

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Varennes A., De Sequeira O.A, 1982. Detection of CM122 latent grapevine virus by enzyme-linked immunosorbent assay (ELISA). Evaluation of short reaction times and re-use of a-globulin and conjugate. *Agronomia Lusitana* **41**: 269-277.

GRAPEVINE CHROME MOSAIC VIRUS (GCMV)

1. DESCRIPTION

GCMV, first found in Hungary near Lake Balaton, was originally called Hungarian chrome mosaic virus and was later recorded from Czechoslovakia, Croatia and Austria. The genome is bipartite. RNA-1 has mol. wt of 2.8×10^6, a size of 7,212 nt and accounts for 40% of the particle weight. RNA-2 has mol. wt of 1.6×10^6, a size of 4.441 nt. and accounts for 31% of the particle weight. The coat protein has a single type of subunits of Mr 52×10^3. Leaves of infected vines are partially or entirely bright yellow or whitish, a symptom virtually indistiguishable from GFLV-induced yellow mosaic. Contrary to the yellow discoluration elicited by chromogenic strains of GFLV, the GCMV-induced yellowing shows on glasshouse-grown vines. Affected vines lack in vigour and may decline and die. Some virus strains induce leaf deformity, double nodes and short internodes, pretty much like *Grapevine fanleaf virus*. However, symptomless infection may occur. The virus belongs in the same subgroup of *Tomato blackring virus* (TBRV, subgroup B) to which is distantly related serologically, and is phylogenetically related also with *Grapevine Anatolian ringspot virus* (GARSV). The hypothesis has been put forward that a recombination between TBRV and GARSV may have generated GCMV. Although GCMV particles have been detected by ELISA in *Xiphinema index* fed on infected hosts, early reports that this nematode could transmit the virus have not been confirmed. GCMV is transmitted through grapevine seeds. Tobacco plants and the rootstock 110R have been successfully transformed with the viral coat protein for induction of resistance.

2. HISTORICAL REVIEW

1965 **Martelli** *et al.*: Host range and properties of a spherical virus, called Hungarian chrome mosaic virus, transmitted to herbaceous hosts from Hungarian grapevines with symptoms similar to those of fanleaf and yellow mosaic. The virus is serologically unrelated to GFLV and is not transmitted by *X. index.*

1965 **Martelli:** Purification and serology of the virus isolated from Hungarian grapevines with fanleaf and yellow mosaic-like symptoms. Confirmation that the virus has no serological relationship with GFLV.

1968 **Martelli** *et al.*: The isometric virus associated with Hungarian chrome mosaic is serologically distantly related to *Tomato black ring virus* (TBRV).

1968 **Jakó** *et al:* HCMV affects pigment and sugar content of infected grapevine leaves.

1969 **Pozsár** *et al.*: HCMV adversely affects photosynthetical carbon dioxide fixation.

1969 **Martelli and Sarospataki**: *X. vuittenezi* is very frequently found in vineyards with chrome mosaic patches, sometimes together with *X. Index.*

1971 **Lehoczky and Tasnady**: A study of the effect of HCMV on yield and sugar content of infected grapevines.

1972a **Martelli and Quacquarelli**: Physico-chemical characterization of HCMV and comparison with TBRV.

1972b **Martelli and Quacquarelli**: Description of HCMV in the CMI/AAB Descripitons of Plant Viruses series. Virus re-named Grapevine chrome mosaic virus.

1972 **Kenten**: GCMV is distantly serologically related to *Cacao necrosis virus.*

1975 **Mali** *et al.*: GCMV recorded from Slovakia and report of *X. index* as vector of the virus (unconfirmed results). No evidence that *X. vuittenezi* transmits GCMV or GFLV.

1977 **Saric and Hranuelli:** GCMV recorded from Croatia.

1979 **Lehoczky** *et al.*: Characterization of a GCMV strain and confirmation of its serological relationship with TBRV.

1980 **Russo** *et al.*: Detection of GCMV in leaf dips by ISEM.

1980 **Roberts and Brown**: Detection of GCMV in *X. index* extracts by ISEM. This finding does not imply vectoring capacity by this nematode.

1982 **Doz** *et al.*: GCMV cross-protects *Chenopodium quinoa* from the severe apical necrosis induced by a TBRV strain.

1984 **Dodd and Robinson**: GCMV and TBRV are molecularly related.

1985 **Kölber** *et al.*: GCMV detected by ELISA in infected field-grown vines.

1985 **Lehoczky**: Pinot noir and Jubileum 75 are good indicators for GCMV.

1989 **Le Gall** *et al.*: Complete nucleotide sequence of GCMV RNA-1.

1989 **Brault** *et al.*: Complete nucleotide sequence of GCMV RNA-2.

1989 **Bretout** *et al.*: Development of molecular probes for GCMV detection.

1990 **Lázár** *et al.*: Seed transmission of GCMV in grapevine.

1993 **Brault** *et al.*: Tobacco plants genetically engineered with the coat protein gene of GCMV are resistant to infection.

1993 **Lehoczky** *et al.*: Description of a certification scheme for the production of virus-free propagating material in Hungary.

1994 **Dimou** *et al.*: GCMV recorded from Austria.

1994 **Le Gall** *et al.*: Transformation of rootstock 110R with the coat protein gene of GCMV. No assessment of resistance made.

1995 **Brandt and Himmler**: Development of a IC-PCR protocol for GCMV detection in cortical scrapings from dormant grapevine canes.

1995 **Le Gall** *et al.*: GCMV and TBRV can recombine. Further demonstration that the two viruses are related.

1997 **Taylor and Brown:** Results of GCMV transmission trials with *X. index* are inconclusive. The virus vector is yet to be identified.

2000 **Lázár** *et al.*: Up-to-date report on virus diseases of grapevines in Hungary and description of the clean stock programme implemented in the country.

2014 **Digiaro** *et al.*: GCMV recognized as a putative interspecies recombinant having *Grapevine Anatolian ringspot virus* and *Tomato black ring virus* as parents. The recombination event is at the movement protein ($2B^{MP}$) level.

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GRAPEVINE DEFORMATION VIRUS (GDefV)

1. DESCRIPTION

Grapevine deformation virus (GDefV) was recovered from Turkish grapevines showing distinct fanleaf-like symptoms. The virus belongs in the subgroup A of the genus *Nepovirus* and is distantly related serologically to ArMV but not to GFLV, the two viruses from whose recombination it originated. Particles are isometric *ca.* 30 nm in diameter and sediment as three components. The genome is bipartite, RNA-1 has a mol. wt of 2.6×10^6 Da, consists of 7,386 nts comprised in a single ORF encoding a polyprotein of 252 kDa. RNA-2 has a mol. wt of 1.3×10^6 Da and a size of 3,753 nt., its single ORF expresses a polypeptide of 123 kDa. Coat protein subunits have a M_r 53×10^3. GDefV is readily detected by ELISA and PCR using primers designed on the coat protein sequence. The virus has no recognized vector, is not seed-borne and occurs in south-eastern Turkey and Iran. The scattered distribution of infected vines in the field suggests that the virus is spread primarily by infected propagative material.

2. HISTORICAL REVIEW

2002 **Cigsar** *et al.***:** First isolation by mechanical transmission of an unknown nepovirus from Turkish vines showing leaf and cane deformations.

2003 **Cigsar** *et al.*: Description and thorough characterization of GDefV, identified as a new species in the subgroup A of the genus *Nepovirus*, distantly serologically related with ArMV.

2005 **Abou Ghanem-Sabanadzovic** *et al.*: Complete nucleotide sequence of GDefV RNA-2.

2012 **Elbeaino** *et al.*: Complete nucleotide sequence of GDefV RNA-1 and demostration that the virus is a recombinant between GFLV and ArMV.

2012 **Hajizadeh** *et al.*: GDefV recorded in Iran.

3. REFERENCES

Abou Ghanem-Sabanadzovic N., Sabanadzovic S., Digiaro M., Martelli G.P., 2005. Complete nucleotide sequence of RNA-2 of two Turkish nepoviruses. *Virus Genes* **30**: 335-340.

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Elbeaino T., Digiaro M., Ghebremeskel S., Martelli G.P., 2012. Grapevine deformation virus: completion of the sequence and evidence on its origin from recombination events between *Grapevine fanleaf virus* and *Arabis mosaic virus*. *Virus Research* **166**: 136-140.

Hajizadeh M., Sokhandan-Bashir N., Elbeaino T., 2012. First report of *Grapevine deformation virus* and *Grapevine Anatolian ringspot virus* in Iran. *Journal of Plant Pathology* **94**: S4.96.

GRAPEVINE TUNISIAN RINGSPOT VIRUS (GTRSV)

1. DESCRIPTION

Grapevine Tunisian ringspot virus (GTRSV), was isolated from a Tunisian grapevine with mild fanleaf-like symptoms. The virus sediments as three components: T (empty shells), M (particles contaning a molecule of RNA-2 with Mol. wt of 2×10^6 daltons and apparent size of *ca.* 5,800 nt) and B (particles containing a molecule of RNA-1 with Mol. wt of 2.4×10^6 daltons and apparent size of *ca*. 6,800 nt.). GTRSV is serologically unrelated to any of 19 nepoviruses tested, including all those known to infect grapevine, and belongs in the subgroup C of the genus *Nepovirus*. No vector is known and no information is available on the distribution and economic importance of the virus.

2. HISTORICAL REVIEW

1991 **Ouertani** *et al.*: A mechanically transmissible virus was recovered by sap inoculation from Tunisian grapevines showing mild fanleaf-like symptoms. Based on its properties the virus appears to be a new nepovirus serologically unrelated to any of 19 members of the genus and has no known vector.

3. REFERENCES

Ouertani R., Savino V., Minafra A., Boscia D., Castellano M.A., Martelli G.P. and Greco N., 1992. Properties of a previously undescribed grapevine nepovirus from Tunisia. *Archives of Virology* **126**: 107-117.

RASPBERRY RINGSPOT VIRUS (RpRSV)

1. DESCRIPTION

Raspberry ringspot virus (RpRSV) is a nepovirus belonging in subgroup A of this genus. Particles are about 30 nm in diameter, have a angular outline, and sediment as three components (T, M, and B). The grapevine strain of this virus is serologically very distantly related to the two main serotypes, Scottish and English, and differs from the type strain as it often sediments as if it were a single centrifugal component. The viral genome is a bipartite positive sense ssRNA, consisting of two separately encapsidated molecules with Mol. wt of 2.6×10^6 (RNA-1) and 1.6×10^6 (RNA-2), accounting for 29% (component M) and 43% (component B) of the particle weight. RNA-2 is 3,928 nt in size and contains a single ORF encoding a polypeptide with M_r of 124 kDa. The coat protein has a single type of subunits with M_r 54×10^3. The virus has been found in grapevine in Germany and Switzerland. A German grapevine isolate and a Swiss isolate have been sequenced totally (Germany) or partially (Switzerland). Both genomic RNAs of the German isolate have structure and composition typical of those of nepoviruses. RNA-1 and RNA-2 are 7,935 and 3,912 nucleotide long, respectively. Phylogenetically, the grapevine strains are very close to each other and are comprised in a subclade distinct from the one that includes all sequenced RpRSV strains recovered from other hosts. Symptoms shown by infected vines are similar to those of fanleaf. Two virus strains of different virulence occur in the Palatinate. Crop losses can be higher than 30%. The type strain of RpRSV is transmitted by *Longidorus macrosoma* but the grapevine strain is transmitted by *Paralongidorus maximus*.

2. HISTORICAL REVIEW

1970 **Vuittenez** *et al.*: Recovery of RpRSV from grapevines of Palatinate.

1978 **Murant:** Description of RpRSV in the CMI/AAB Plant Virus Description series.

1978 **Stellmach and Querfurth:** Study of a strain of RpRSV isolated from cv. Elbling in West Germany. FS4 is a good indicator. Heat therapy of infected grapevines.

1982 **Brückbauer:** RpRSV can be distinguished from other nepoviruses on the basis of symptoms induced on *Vitis* idicator plants.

1992 **Blok** *et al.*: Nucleotide sequence of RpRSV RNA-2.

1994 **Jones** *et al.*: Biological and physico-chemical characterization of the grapevine strain of RpRSV. This strain differs considerably from the English type strain of the virus although is serologically closely related to it. The virus is transmitted by *Paralogidorus maximus.*

2003 **Ebel** *et al.:* Sequencing and molecular characterization of two German isolates of RpRSV from grapevine.

2006 **Wetzel** *et al.*: A German grapevine isolate of *Raspberry ringspot virus* (RpRSV) and a Swiss isolate of the same virus sequenced totally (Germany) or partially (Switzerland).

3. REFERENCES

Blok V.C., Wardell J.,. Jolly C.A, Manoukian A., Robinson D.J., Edwards M.L.,. Mayo M.A, 1992. The nucleotide sequence of RNA-2 of raspberry ringspot nepovirus. *Journal of General Virology* **73**: 2189-2194.

Brückbauer H., 1982. Mögliche Beziehungen zwischen Virus und Symptomausprägung bei der Rebe. *Die Wein-Wissenschaft* **37**: 88-118.

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Vuittenez A., Kuszala J., Rüdel M., Brückbauer H., 1970. Détection et étude selogique du virus latent des taches annulaires du frasier (strawberry latent ringspot), du virus des anneaux noires de la tomate (tomato black ring) et du virus des taches annulaires du framboisier (raspberry ringspot) chez des vignes du Palatinat. *Annales de Phytopathologie* **2**: 279-327

Wetzel T., Ebel R., Moury B. Le Gall O., Endisch S., Reustle G.M., Krczal G., 2006. Sequence analysis of grapevine isolates of Raspberry ringspot nepovirus. *Archives of Virology* **151**: 599-606.

TOMATO BLACK RING VIRUS (TBRV)

1. DESCRIPTION

Tomato black ring virus (TBRV) was first found in grapevines in Germany, then in Yugoslavia, Greece, Israel, Turkey, and Ontario (Canada). As to other crops, apart form Europe, records exist from Brazil, India, Japan and Kenya. The virus is a definitive nepovirus species classified in subgroup B of this genus. Virus particles are isometric, about 30 nm in diameter have angular outline and sediment as three components (T, M, and B). Their coat protein consists of a single type of subunits with Mr of about 57 kDa. The genome is a bipartite positive sense single-stranded RNA occurring as two separately encapsidated functional molecules with mol. wt of 2.7×10^6 (RNA-1) and 1.65×10^6 (RNA-2) accounting for 44% and 37% of the particle weight, respectively. RNA-1 is 7,356 nt in size and contains a single open reading frame encoding a polypeptide with M_r of 254 kDa. RNA-2 is 4,662 nt in size and codes for a polyprotein with M_r of 150 kDa. TBRV supports the replication of a satellite RNA with mol. wt of 0.5×10^6 daltons and a size of 1,327 nt. Some virus isolates possess smaller RNA-1 molecules (defective RNAs) that my interfere with the replication of the parental genome. Symptoms of infected vines consist of a reduction in growth and yield, chlorotic spots, rings and lines on the leaves of recently infected plants, mottling of older leaves, and increased graft failure. The vector to grapevine is *Longidorus attenuatus.* Crop losses are reported as high, although no precise assessment has apparently been made. Joannes Seyve virus, known to cause severe damage to the grapevine cv. Joannes Seyve in Ontario, is a strain of TBRV.

2. HISTORICAL REVIEW

1963 **Stellmach and Bercks**: TBRV detected in rootstock Aramon x *V. riparia* 143 A in West Germany.

1965 **Stellmach and Bercks**: Further investigations on TBRV in grapevine.

1966 **Bercks and Stellmach**: ArMV, RpRV and TBRV detected serologically in grapevine in West Germany, either by agar gel diffusion with extracts of herbaceous hosts previously infected mechanically from grapevine, or directly in grapevine leaf extracts using bentonite flocculation test.

1967 **Bercks:** Comparison of three serological tests for detecting several viruses, including TBRV: bentonite flocculation test, latex test and barium sulfate

test. The latex test is considered as the most sensitive and the least time consuming method.

1970 **Vuittenez** *et al.*: RRV, SLRV and TBRV found in grapevine in the Palatinate.

1976 **Bercks and Querfurth**: GFLV, ArMV, RRV and TBRV are not transmitted by contact of roots or foliage in the vineyard.

1977 **Rüdel**: Transmission of TBRV to grapevine by *Longidorus attenuatus.*

1980 **Tanne**: Detection of TBRV by ELISA in Israel.

1984 **Stobbs and Van Schagen**: First record of TBRV from Canada. The virus was detected in grapevines in the Niagara Peninsula, as the cause of severe damage to cv. Joannes Seyve.

1984 **Meyer** *et al.*: Nucleotide sequence of a TBRV satellite RNA.

1986 **Lehoczky and Burgyan**: Occurrence of TBRV in grapevines in Hungary.

1986 **Meyer** *et al.*: Nucleotide sequence of RNA-2 of a TBRV strain later identified as the new species *Beet ringspot virus.*

1988 **Greif** *et al.*: Nucleotide sequence of RNA-1 of a TBRV strain later identified as the new species *Beet ringspot virus.*

1993 **Abkas and Erdiller:** TBRV recorded from grapevines in Turkey.

1999 **Pacot-Hiriat** *et al.*: A truncated form of TBRV coat protein confers resistance to transformed tobacco plants.

2004 **Jończyk** *et al.*: Complete sequence of a TBRV strain from Poland.

2010 **Harper** *et al.*: Detection of TBRV by real-time RT-PCR.

2012 **Haslów-Jaroszewska** *et al.*: Defective RNA-1 found in TBRV.

2014 **Digiaro** *et al.*: Complete sequence of a grapevine TBRV isolate.

3. REFERENCES

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Greif C., Hemmer O., Fritsch C., 1988. Nucleotide sequence of Tomato black ring virus RNA-1. *Journal of General Virology* **69**: 1517-1529.

Harper S.J., Delmiglio C. Ward L.I., Clover G.R.G., 2011. Detection of Tomato black ring virus by real-time one-step RT-PCR. *Journal of Virological Methods* **171**: 190-194.

Haslów-Jaroszewska B., Borodynko N., Figlerowicz M., Pospieszny H., 2012. Two types of defective RNAs arising from Tomato black ring virus genome. *Archives of Virology* **157**: 569-572.

Jończyk M., Le Gall O., Pałucha A., Borodynko N., Pospieszny H., 2004. Cloning and sequencing of full-length cDNAs of RNA1 and RNA2 of a *Tomato black ring virus* isolate from Poland. *Archives of Virology* **149**: 799-807.

Meyer M., Hemmer O., Fritsch C., 1984. Complete nucleotide sequence of a satellite RNA of Tomato black ring virus. *Journal of General Virology* **65**: 1575-1583.

Meyer M., Hemmer O., Mayo M.A., Fritsch C., 1986. The nucleotide sequence of Tomato black ring virus RNA-2. *Journal of General Virology* **67**: 1257-1271.

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Stobbs L.W., Van Schagen J.G., 1984. Occurrence of Tomato black ring virus on grapevine in southern Ontario. *Canadian Plant Disease Survey* **64**: 3-5.

Vuittenez A., Kuszala J., Rüdel M., Brückbauer H., 1970. Détection et étude sérologique du virus latent des taches annulaires du Fraisier (strawberry latent ringspot), du virus des anneaux noirs de la tomate (tomato black ring), et du virus des taches annulaires du framboisier (raspberry ringspot) chez des vignes du Palatinat. *Annales de Phytopathologie* **2**: 279-327.

FAMILY *SECOVIRIDAE*: UNASSIGNED SPECIES

STRAWBERRY LATENT RINGSPOT VIRUS (SLRSV)

1. DESCRIPTION

SLRSV has been isolated from grapevine in the Palatinate (Germany) and in northern Italy. It was also detected in imported vines in Turkey and Portugal. The taxonomic position of this virus has changed from a tentative assignment to the genus *Nepovirus*, to a species in the genus *Sadwavirus*, to the current allocation as unassigned species in the family *Secoviridae.* Virus particles are isometric, about 30 nm in diameter have angular outline and sediment as three components (T, M, and B). Their coat protein consists of two types of subunits with M_r 43×10^3 and 27×10^3, respectively. The genome is a bipartite positive sense single-stranded RNA occurring as two separately encapsidated functional molecules with mol. wt 2.6×10^6 (RNA-1) accounting for 38% of the particle weight, and 1.6×10^6 (RNA-2). RNA-1 is 7,496 nt in size, and consisté of a single ORF. RNA-2 is 3,824 nt in size and encodes a single ORF expressing a polypetide with M_r of about 99

kDa. The virus supports the replication of a satellite RNA 1,118 nt in size. Symptoms on affected European grapes are of the fanleaf type. The virus is transmitted by *Xiphinema diversicaudatum.*

2. HISTORICAL REVIEW

1974 **Murant**: Description of SLRSV in the CMI/AAB Descriptions of Plant virus series.

1977 **Bercks** *et al.*: SLRSV and other nepoviruses isolated from grapevines in Germany.

1981 **Credi** *et al.*: SLRSV recorded from grapevine in Italy.

1982 **Babini and Bertaccini**: Electron microscope study SLRSV infections in plant tissues.

1982 **Brückbauer**: SLRSV can be distinguished from other nepoviruses on the basis of symptoms induced on *Vitis* idicator plants.

1987 **Savino** *et al.*: SLRSV found in grapevine in Turkey.

1993 **Kreiah** *et al.*: Nucleotide sequence of SLRSV satellite RNA.

1994 **Kreiah** *et al.*: Nucleotide sequence of SLRSV RNA-2.

2005 **Le Gall** *et al.* Assignement of SLRSV to the new genus *Sadwavirus.*

2011 **Sanfaçon** *et al.*: Re-assigment of SLRSV as unassigned species in the family *Secoviridae.*

3. REFERENCES

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Brückbauer H., 1982. Mögliche Beziehungen zwischen Virus und Symptomausprägung bei der Rebe. *Die Wein-Wissenschaft* **37**: 88-118.

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Sanfaçon H., Iwanami T., Karasev A.V., van der Vlugt R., Wellink J., Wetzel T., Yoshikawa, N., 2011. Family *Secoviridae.* In: King A.M.Q., Adams M.J., Carstens E.B., Lefkowitz E.J. (eds). Virus Taxonomy. Ninth Report of the International Committee on the Taxonomy of Viruses, pp. 881-899. Elsevier/Academic Press, Amsterdam, The Netherlands.

Savino V., Martelli G.P., D’Onghia A.M., Yilmaz M.A., 1987. Turkey. Strawberry latent ringspot virus in grapevine. *FAO Plant Protection Bulletin* **35:** 102-104.

GRAPEVINE DEGENERATION AND DECLINE (AMERICAN NEPOVIRUSES)

1. DESCRIPTION.

Main synonyms: Yellow vein, grapevine decline, little grape (Eng.), jaunissement des nervures, depérissement de la vigne (Fr.), Adernvergilbung (Germ.), deperimento della vite, ingiallimento nervale (Ital.)

Main symptoms: Symptomatological responses of grapevines vary according to the species (i.e. *Vitis vinifera, V. labrusca,* interspecific hybrids), the infecting virus and the climatic conditions. In cold climates [e.g. New York State (USA) and Ontario (Canada)] own-rooted European grapes affected by *Tomato ringspot virus (*ToRSV) and *Tobacco ringspot virus* (TRSV) decline rapidly, exhibiting stunted growth, mottled (oak leaf pattern, and/or ringspots) and distorted leaves, distortion of canes, poor fruit setting, straggly and shelled clusters. In warmer climates [Maryland, California (USA)] yield but not vigour is affected. Bunches are small and straggly (Maryland's grapevine little berry) and leaves may show chrome yellow flecking along the veins (California's yellow vein). *Peach rosette mosaic virus* (PRMV) in *V. labrusca* causes a severe disease characterized by delayed bud burst, malformation and mottling of the leaves, and poor fruit set. Infected vines decline slowly over time. *Blueberry leaf mottle virus* (BLMoV) infects latently European grapes, whereas in *V. labrusca* cv. Concord it delays bud burst, induces fanleaf-like symptoms on leaves and canes, and poor fruit setting.

Agent: The above mentioned four distinct nepoviruses, BLMoV, TRSV, PRMV, and ToRSV separately or in combination, are involved in the aetiology of North American grapevine degeneration and decline. All these viruses, except for BLMoV which may have been introduced from Europe, are endemic in North America and thought to be native of the region.

Transmission: All these viruses are transmitted by grafting and mechanical inoculation. No vector is known for BLMoV, which in blueberry is transmitted by pollen. All other viruses are transmitted by longidorid nematodes: *Xiphinema americanum sensu stricto* and *X. rivesi* transmit ToRSV type strain (decline), *X. californicum* transmits ToRSV yellow vein strain. TRSV is transmitted by *X. americanum sensu lato* and PRMV by *X. americanum sensu stricto, Longidorus diadecturus* and *L. elongatus.* PRMV, ToRSV and BLMoV are also seed-transmitted in grapes. Alternative weed hosts that have epidemiological significance are known for ToRSV, TRSV and PRMV. Long distance spread takes place primarily through infected propagating material.

Varietal susceptibility: There are great variations in the susceptibility of *Vitis* species and cultivars. A number of rootstocks containing *V. riparia, V. berlandieri* or *V. rupestris* plasma show field resistance to the northern US strain of ToRSV and to TRSV and PRMV. *V. labrusca* is also resistant to TRSV. This type of resistance is hypersensitivity. All roostocks and, interestingly, most *V. vinifera* cultivars are reported as being immune to the Californian strain of ToRSV.

Detection: All viruses are transmissible to herbaceous hosts mechanically and to woody indicators by grafting, ELISA and molecular tools (hybridization, various PCR protocols) are used for testing field-infected material.

Control: Use of virus-free propagating material and resistant rootstocks. Nematicidal control of vectors was possibile until these chemicals were in use. Fumigations, however, were not conclusive.

BLUEBERRY LEAF MOTTLE VIRUS (BLMoV)

1. DESCRIPTION

Blueberry leaf mottle virus (BLMoV) is named after the disease induced in highbush blueberry (*Vaccinium corymbosum)*, its main host. BLMoV is a definitive nepovirus species assigned to subgroup C. Virus particles are isometric, about 30 nm in diameter with angular outline, sedimenting as three components. Their coat protein consists of a single type of subunits with M_r of about 54×10^3 Da. The genome is a bipartite, positive-sense, single-stranded RNA occurring as two separately encapsidated functional molecules with mol. wt of 2.35×10^6 (RNA-1) and 2.15×10^6 (RNA-2). The partial sequence of the 3' termini of both RNA molecules has been determined. Grapevines (*Vitis labrusca*) are infected in New York State (USA) by a

serologically distinct strain of the virus, which induces fanleaf-type symptoms and is distantly related to *Grapevine Bulgarian latent virus* (GBLV). The virus is seed-transmitted in grapevines and *C. quinoa,* and has no economic importance. The vector is unknown, but in highbush blueberry the virus is pollen-borne and suspected to be pollen-transmitted.

2. HISTORICAL REVIEW

1977 **Uyemoto** *et al*: BLMoV isolated from New York cv. Concord vines showing fanleaf-like symptoms, and identified as a strain of GBLV. The virus is transmitted through seeds in grapevines and *C. quinoa.*

1981 **Ramsdell and Stace-Smith:** Physico-chemical characterization of BLMoV and evidence that the New York grapevine virus is a strain of BLMoV.

1994 **Bacher** *et al*.: Partial nucleotide sequence of BLMoV RNA-1 and RNA-2.

3. REFERENCES

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PEACH ROSETTE MOSAIC VIRUS (PRMV)

1. DESCRIPTION

Peach rosette mosaic virus (PRMV) is named after the disease induced in peach, one of its plant hosts. The virus is a definitive nepovirus species assigned to subgroup C. Virus particles are isometric, about 28 nm in diameter with angular outline, sedimenting as three components. Their coat protein consists of a single type of subunits with M_r of about 57×10^3 Da. The genome is a bipartite positive sense single-stranded RNA occurring as two separately encapsidated functional molecules with mol. wt of 2.4×10^6 (RNA-1) and 2.2×10^6 (RNA-2) accounting for 44% and 37% of the particle weight, respectively. RNA-1 is 8,004 nt in size and contains a single open reading frame encoding a polypeptide with M_r of 240 kDa. As yet, RNA-2 has not been sequenced. Infected grapevines show shortened and crooked shoots, mottled and variously deformed leaves and delayed bud burst. Clusters are straggly, smaller and fewer than normal, and with extensive shelling of the berries. Vines are stunted and show a progressive decline, which may lead to their death. PRMV is soil-borne. Healthy grapevines become infected when planted in soils of diseased vineyards, where the disease occurs in more or less circular patches and spreads slowly, mostly to vines adjacent to previously infected plants. Vectors are the Dorylaimoid nematodes *Xiphinema americanum sensu lato* and *Longidorus diadecturus.* Occasional, possibily non specific transmission by *L. elongatus* has also been reported. As the virus is endemic and seed-borne in the perennial weeds *Taraxacum officinale* (dandelion), *Solanum carolinense* (Carolina horse nettle) and *Rumex crispus* (curly dock), when a vineyard is planted susceptible cultivars may become infected by nematode vectors. PRMV can also be introduced in a site by infected planting material and be spread by vectors to adjacent vines. Pollen grains of cv. Concord grapes are apparently virus-free but 9.5% of the seedlings from seeds taken from diseased vines proved to be infected. PRMV is seed-borne in both naturally infected dandelion (4% of infected seedlings) and in artificially infected *C. quinoa* (90% infected seedlings). Crop losses up to 60% and death of susceptible *V. labrusca* cultivars (Concord, especially) and a number of American-French hybrids have been recorded. Prolonged fallow is not an effective means of control because viruliferous nematodes remain alive for many years thriving on infected surviving roots and alternative weed hosts. Roguing of infected vines and preplanting autumn fumigation with high rates of fumigant injected at two depths (15-20 cm and 75-90 cm) can effectively reduce, but not eradicate, vector populations. Use of resistant roostock hybrids and of certified planting material is recommended.

2. HISTORICAL REVIEW

1972a **Dias**: Preliminary characterization of the grapevine isolate of PRMV.

1972b **Dias:** Grapevine and peach strains of PRMV can be differentiated serologically.

1974 **Ramsdell and Myers**: Description of PRMV-induced grapevine degeneration and association of *X. americanum* with the disease.

1976 **Dias and Cation**: Biological characterization of the grapevine strain of PRMV. The virus is seed-borne in *C. quinoa* and has reproduced in part the field syndrome when inoculated mechanically to Concord grape seedlings.

1978 **Ramsdell and Myers**: Field spread of PRMV is associated with the presence of infected weeds (*T. officinale, S. carolinense, R. crispus*) and transmission through grape seeds.

1979 **Ramsdell** *et al:* Use of ELISA for PRMV detection in grapevines.

1980 **Dias and Allen**: Physico-chemical characterization of PRMV.

1982 **Allen** *et al.*: *Longidorus diadecturus* transmits PRMV to grapevines.

1983 **Ramsdell** *et al:* High rates of fumigant injected at two depths (15-20 cm and 75-90 cm) during autumn reduce effectively but do not eradicate nematode vector populations in infested soils.

1984 **Allen** *et al.*: *Xiphinema americanum* is an efficient vector of PRMV.

1985 **Ramsdell and Gillet:** List of grapevine cultivars and roostocks showing differential susceptibility to PRMV.

1988 **Ramsdell:** Review article on PRMV.

1988 **Allen and Ebsary:** *Longidorus attenuatus* transmits PRMV non specifically and with low efficiency.

1995 **Ramsdell** *et al.*: Investigation on the susceptibility to PRMV infection of American and European grapevines and hybrid rootstocks.

1998 **Ramsdell and Gillet**: Description of PRMV in the AAB Descriptions of Plant Viruses series.

1999 **Lammers** *et al.*: Nucleotide sequence of RNA-1 of the grapevine strain of PRMV.

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TOBACCO RINGSPOT VIRUS (TRSV)

1. DESCRIPTION

Tobacco ringspot virus (TRSV) is the type species of the genus *Nepovirus* and the prototype of subgroup A. Virus particles are isometric, about 30 nm in diameter with angular outline, sedimenting as three components (T, M, and B). Coat protein consists of a single type of subunits with M_r of about 57×10^3 Da. The genome is a bipartite positive-sense single-stranded RNA occurring as two separately encapsidated functional molecules with mol. wt of 2.7×10^6 (RNA-1) and 1.3×10^6 (RNA-2), accounting for 44% and 28% of B and M particle weight, respectively. RNA-1 is 7,514 nt in size and contains a single open reading frame encoding a polypeptide with Mr of 225 kDa. RNA-2 has been sequenced only in part. The virus supports the replication of a circular satellite RNA 359 nt in size. TRSV has a relatively wide natural host range, is endemic in Central and Eastern North America, but has been recorded from grapevines only in New York state and Pennsylvania. Symptoms elicited by TRSV are the same as those of ToRSV in native cultivars, but in European grapes

responses are similar to those elicited by GFLV. TRSV is soil-borne and is transmitted by *Xiphinema americanum sensu stricto*. There is no evidence of seed trasmission in the grapevine. Preventive control measures are the use of resistant roostock hybrids and of certified planting material.

2. HISTORICAL REVIEW

1970 **Gilmer** *et al.*: TRSV agent of a new grapevine disease in New York State.

1977 **Uyemoto** *et al.*: A review of viruses infecting grapevines in New York vineyards. American *Vitis* species reported to be resistant to ToRSV and TRSV.

1985 **Stace-Smith:** Description of TRSV in the AAB Descriptions of Plant Viruses series.

1985 **Foster and Morris-Krsinich**: *In vitro* translation of TRSV RNA-1 and TRSV RNA-2 yields major polypeptides with Mr of 225K and 116K, respectively.

1986 **Buzayan** *et al.*: Nucleotide sequence of TRSV satellite RNA.

1990 **Powell** *et al.*: Survey of ToRSV and TRSV in Pennsylvanian vineyards.

1993 **Buckley** *et al.*: Partial nucleotide sequence of TRSV RNA-2.

1996 **Zallua** *et al.*: Complete nucleotide sequence of TRSV RNA-1.

2009 **Martin** *et al*: Use of collagenase dissolves nematode (*X. americanum*) cuticle and enables TRSV RNA extraction for subsequent amplification by RT-PCR.

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TOMATO RINGSPOT VIRUS (ToRSV)

1. DESCRIPTION

Tomato ringspot virus (ToRSV) is a definitive species in the genus *Nepovirus* and the prototype of subgroup C. Virus particles are isometric, about 30 nm in diameter with angular outline, sedimenting as three components (T,M, and B). Coat protein consists of a single type of subunits with M_r of about 58×10^3 Da. The genome is a bipartite positive-sense single-stranded RNA occurring as two separately encapsidated functional molecules with mol. wt of 2.8×10^6 (RNA-1) and 2.4×10^6 (RNA-2) accounting for 44% and 41% of the particle weight, respectively. RNA-1 is 8,214 nt and RNA-2 is 7,273 nt in size. Both RNAs contain a single open reading frame encoding polypeptides with Mr of 244 kDa (RNA-1) and 207 kDa (RNA-2). ToRSV has a relatively wide natural host range and is endemic in North America, where it occurs in the region of the Great Lakes and in the Pacific seaboard from California to British Columbia. The virus has been occasionaly recorded from grapevines outside of North America. Two serological ToRSV variants are known to infect grapevines. Symptomatological responses vary according to the species (*V. vinifera, V. labrusca*, interspecific hybrids), the infecting virus strain, and the climatic conditions. ToRSV-induced decline affects European cultivars, especially if self-rooted, more severely in colder than in warmer climates. Infected vines have small, mottled and distorted leaves and short internodes. Clusters are straggly, smaller and fewer than normal, and with extensive shelling of the berries. Vines are stunted and show a progressive rapid decline, which often leads to death. In California ToRSV affects the yield rather than the vine's growth, "yellow vein" being the characterizing syndrome of its infections. Vines grow vigorously but bear little or no fruit. ToRSV is soil-borne. Vectors are the Dorylaimoid nematodes *Xiphinema americanum sensu stricto* and *X. rivesi* in northern USA states and Canada and *X. californicum* in California. The virus can be introduced in a site by infected planting material and be spread by vectors to adjacent vines. The yellow vein strain of the virus is pollen-borne but is not transmitted through seeds; contrary to the decline strain which

is seed-transmitted. Preventive control measures are the use of resistant roostock hybrids and of certified planting material.

2. HISTORICAL REVIEW

1954 **Hewitt**: Report of an "unfruitful vine" condition in California to which a yellow speckling of the leaves is associated.

1956 **Hewitt:** Successful graft transmission of unfruitful vine condition. Disease named yellow vein.

1962 **Gooding and Hewitt:** A mechanically transmissible virus found to be associated with yellow vein.

1963 **Gooding**: Yellow vein virus identified as a strain of ToRSV.

1966 **Teliz** *et al.*: Transmission of the yellow vein strain of ToRSV by *X. americanum* (now *X. californicum*).

1968 **Cory and Hewitt:** The yellow vein strain of ToRSV is not transmitted through seeds.

1972 **Gilmer and Uyemoto**: ToRSV agent of a decline of Baco noir in New York State.

1972 **Uyemoto and Gilmer**: Spread of ToRSV through the soil of New York State vineyards recorded.

1975 **Uyemoto**: Seed transmission of the decline strain of ToRSV.

1977 **Dias**: ToRSV in the Niagara peninsula.

1977 **Uyemoto** *et al.*: A review of viruses infecting grapevines in New York State vineyards. American *Vitis* species reported to be resistant to ToRSV and TRSV.

1977 **Allen and Dias**: Physico-chemical characterization of ToRSV

1978 **Martelli**: Review of nematode-borne viruses of grapevines and their epidemiology.

1980 **Gonsalves**: ToRSV is irregularly distributed in infected vines but can be detected by ELISA.

1982 **Podlekis and Corbett:** ToRSV is the agent of little grape disease in Maryland.

1982 **Allen** *et al.*: List of grapevine roostocks and cultivars showing differential susceptibility to ToRSV in Canada.

1984 **Stace-Smith**: Description of ToRSV in the CMI/AAB Descriptions of Plant Viruses series.

1985 **Piazzolla** *et al.*: Confirmation that the grape yellow vein and the the grape decline strains of ToRSV are serological variants of the same virus.

1985 **Corbett and Podleckis**: Ultrastructural study of ToRSV-infected grapevine tissues.

1986 **Yang** *et al.*: ToRSV found in grapevines in Taiwan.

1987 **Stace-Smith and Ramsdell:** Review of nepoviruses of the Americas.

1987 **Bitterlin and Gonslaves:** ToRSV retained and transmitted by viruliferous *Xiphinema rivesi* stored for two years at 1-3°C.

1988 **Allen** *et al.*: *Xiphinema rivesi* identified as the main vector of ToRSV in Ontario vineyards.

1989 **Martelli and Taylor**: Review of nematode-borne viruses and their vectors.

1989 **Bays and Tolin**: ToRSV in grapevines in Virginia.

1990 **Powell** *et al.*: Survey of ToRSV and TRSV in Pennsylvanian vineyards.

1991 **Rott** *et al.*: Complete nucleotide sequence of ToRSV RNA-2.

1992 **Rowhani** *et al:* Description of sampling strategy for detection of ToRSV.

1993 **Baumgartnerova and Subikova**: ToRSV recorded form grapevine in Slovakia.

1995 **Rott** *et al.*: Complete nucleotide sequence of ToRSV RNA-1.

2001 **Herrera and Madariaga**: ToRSV recorded from grapevine in Chile.

2004 **Li** *et al:* ToRSV identified in China in grapevine seedlings grown from seeds imported from France.

2004 **Pourrahim** *et al.*: ToRSV in Iran.

2006 **Sanfaçon** *et al.*: Review article on the molecular biology of ToRSV.

2007 **Stewart** *et al.*: Development of a real-time RT-PCR SYBR green assay for ToRSV detection in grapevines.

2008 **Osman** *et al.*: Use of Taq-Man low density array (LDA) for sensitive detection of grapevine-infecting viruses among which ToRSV.

2011 **Li** *et al.*: The 5' and 3' untranslated sequences (UTR) of ToRSV isolates are 1.3 nts in size and virtually identical. RT-PCR using primers designed within the highly conserved 3' UTR regions detected 20 ToRSV isolates including two from a vineyard. This assay can serve for the sensitive detection of varied ToRSV isolates as it is more sensitive than a RT-PCR assay based on previously reported U1/D1 primers.

2013 **Sanfaçon**: Review article on the role of viral integral membrane proteins in the assembly of nepovirus replication factories with reference also to ToRSV.

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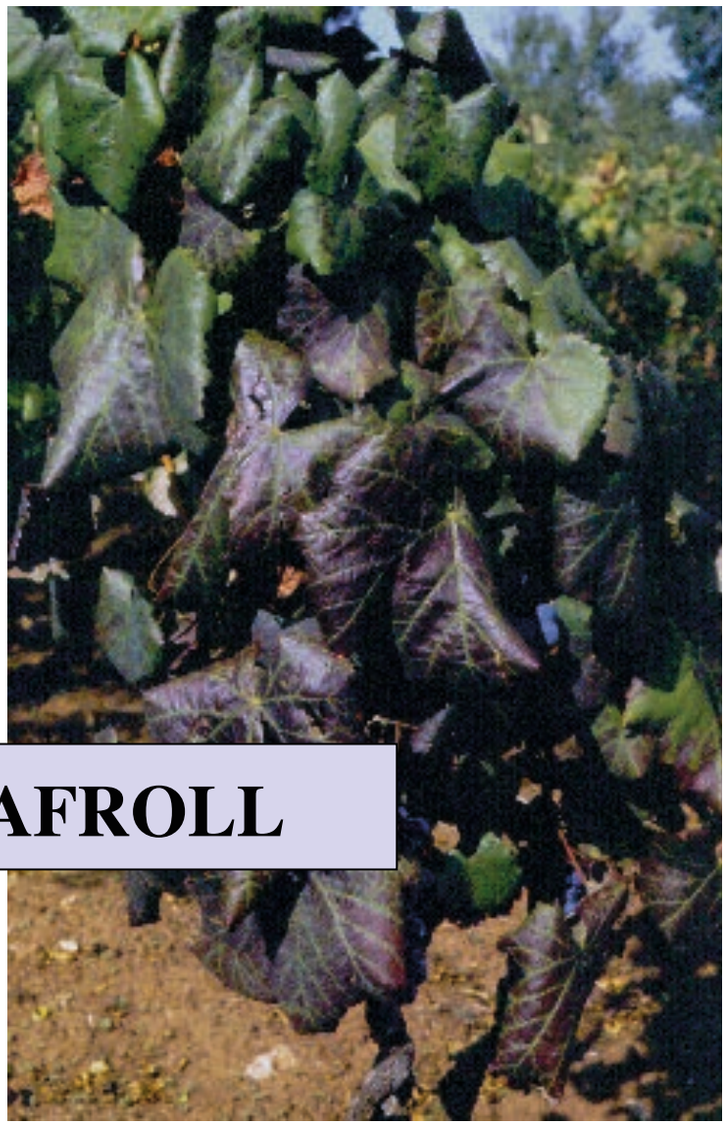

LEAFROLL

GRAPEVINE LEAFROLL

1. DESCRIPTION.

The first descriptions of grapevine leafroll date back to the mid 19th century. There are reports of early reddening of grapevine leaves regarded as physiological disorders and referred to as "Rugeau" or "Rossore" in the French and Italian literature, respectively. Leafroll is no less important than fanleaf in economic importance, and appears to be the most widespread virus disease of grapevine.

Main synonyms: White Emperor disease (Eng.), Rollkrankheit, Blattrollkrankheit (Germ.), enroulement (Fr.), accartocciamento, accartocciamento fogliare (Ital.), enrollamiento de la hoja, enrollado (Sp.), Enrolamento de la folha (Port.)

Main symptoms: In red-berried cultivars of *Vitis vinifera* reddish spots develop in the lower leaves in late spring or summer, depending on the climate and geographic location. These spots enlarge with time and coalesce so that, in autumn, most of the leaf surface becomes reddish, usually leaving a narrow green band along the primary and secondary veins. The leaf blade becomes thick, brittle and rolls downwards. These symptoms progress towards the top of the vines as the season advances. In the most severe cases and very late in the season, the whole leaf surface becomes deep purple. The fruits often mature late and irregularly, and with many cultivars, they are inferior in quantity and quality, and low in sugar. In white-berried cultivars of *V. vinifera*, the symptoms are similar, but the leaves become chlorotic to yellowish, instead of reddish. Careful observation of field symptoms in infected vines reveals that there are several types of leafroll, differing somewhat in aspect and in severity, thus suggesting that there can be several causal agents. In most cases, infection of rootstocks is symptomless, except for a variable decrease in vigour. Hence, the risk of disseminating the disease is great if untested rootstocks are used. Leafroll decreases grapevine yield (by 15-20% in average, with peaks of up 40%) and affects negatively rooting ability, graft take, plant vigour, photosynthesis, as well as modulation of host genes involved in a variety of biological functions. The economic impact of leafroll disease was estimated to range from US$ 25,000 to US$ 40,000 per hectare for vineyards with a 25-year lifespan in the Finger lakes region of New York State (USA). Roguing, identified as an economically important practice, can significantly decrease economic losses together with planting of virus-free plant material. Plant anatomy is also affected, especially the phloem. Sieve elements are obliterated and crushed thus impairing

Classification as to 2011 and some properties of Grapevine leafroll-associated viruses (GLRaVs).

Virus	Genus	Coat protein (kDa)	Genome size (nts) (GenBank access. No.)	ORFs (No.)	Vectors	First record *fide* Boscia *et al.* (1995); Martelli *et al.* (2012)
GLRaV-1	*Ampelovirus*	34	18,659 (JQ023131)	9	Mealybugs, soft scale insects	Gugerli *et al.* (1984)
GLRaV-2	*Closterovirus*	22	16,494 (AY88162)	8	Unknown	Zimmermann *et al.* (1990)
GLRaV-3	*Ampelovirus*	35	18,498 (EU259806)	12	Mealybugs, soft scale insects	Zee *et al.* (1987)
GLRaV-4	*Ampelovirus*	35	13,830 (FJ467503)	6	Mealybugs	Hu *et al.* (1990)
GLRaV-5	*Ampelovirus*	35	13,384[a] (FR822696)	6	Mealybugs	Zimmermann *et al.* (1990); Walter and Zimmermann (1991)
GLRaV-6	*Ampelovirus*	35	13,807 (FJ467504)	6	Mealybugs	Gugerli and Ramel (1993); Gugerli *et al.* (1997)
GLRaV-7	Unassigned in the family	37	16,496 (HE588185)	10	Unknown	Choueiri *et al.* (1996)
GLRaV-8[b]	*Ampelovirus*	37	ND	ND	Unknown	Monis (2000)
GLRaV-9	*Ampelovirus*	35	12,588[a] (AY29781)	6	Mealybugs	Alkowni *et al.* (2004)
GLRaV-Pr	*Ampelovirus*	30	13,696 (AM182328)	6	Mealybugs	Maliogka *et al.* (2009);
GLRaV-Car	*Ampelovirus*	29	13,626 (FJ907331)	6	Unknown	Abou Ghanem-Sabanadzovic *et al.* (2010)

[a] Nearly complete sequence; [b] Cancelled from the 9th ICTV Report (Martelli *et al.*, 2012a); ND, not determined.

carbohydrate translocation from foliar parenchymas. Starch accumulates in degenerated chloroplasts causing increased thickness and brittleness of the leaf blades, and lowering of sugar content. A number of other physiological parameters are affected, i.e. reduction of protein content, changes in the pattern of peroxidase and polyphenoloxidase isoenzymes, potassium depletion in the leaf blade and accumulation in the petioles. Also the composition and aromatic profile of the musts are modified. These negative effects are reverted to a large extent, if not totally, when the disease is eliminated by sanitation treatments.

Agents: Up to 2011, eleven different viruses with filamentous particles, called grapevine leafroll-associated viruses all belonging to the family *Closteroviridae*, nine of which differentiated from one another by a progressive Arabic numeral were thought to be involved in leafroll disease aetiology.

The identification of the single viruses as diverse species was largely determined by the apparent lack of serological relatedness among them and by the scarce molecular information that did not permit a comparison based on more solid parameters. The production of new sets of antisera and the sequencing of the whole genome of all GLRaVs has recently shown that GLRaV-4, -5, -6, and -9 are in fact the same virus, thus allowing a critical revision of the classification of these viruses, that led to a reduction of their number and to a novel taxonomic configuration:

Genus *Closterovirus*
Grapevine leafroll-associated virus 2 (GLRaV-2)

Genus *Ampelovirus*
Grapevine leafroll-associated virus 1 (GLRaV-1)
Grapevine leafroll-associated virus 3 (GLRaV-3)
Grapevine leafroll-associated virus 4 (GLRaV-4)
GLRaV-4 strain 5
GLRaV-4 strain 6
GLRaV-4 strain 9
GLRaV-4 strain Pr
GLRaV-4 strain Car

Genus *Velarivirus*
Grapevine leafroll-associated virus 7 (GLRaV-7)

The discovery that the sequence of Grapevine leafroll-associated virus 8 (GLRaV-8) rather than being of viral origin is part of the grapevine genome, prompted the removal of this virus from the membership of the genus *Ampelovirus*, thus reducing to 5 in three distinct genera the number of GLRaVs. A potyvirus isolated in Israel from leafroll-infected vines is now regarded as an occasional contaminant. Particles of GLRaVs are very flexuous filaments about 12 nm wide, exhibiting open structure and distinct cross banding with a pitch of about 3.5 nm. Particle length varies from 1400 to 2000 nm according to individual viruses, the same as the size of coat protein (CP) subunits. GLRaV-2 CP has a Mr of 24 kDa, whereas the Mr of all other viruses ranges between 35 and 44 kDa, as estimated by polyacrylamide gel electrophoresis. Sizes deduced from the nucleotide sequence of the CP cistron are 22 kDa for GLRaV-2, 35 kDa for both GLRaV-3 and GLRaV-1, 29.5 kDa for GLRaV-4. The genome of all GLRaVs is a monopartite, single-stranded, positive sense RNA molecule. In particular, The genome of GLRaV-2 is 15,528 nt in size, contains eight open reading frames (ORF) and has structural organization identical to that of *Beet yellow virus* (BYV), the type strain of the genus. GLRaV-3, the type species of the genus *Ampelovirus*, has a genome 18,498 (South African isolate) to 18,563 (Chinese isolate) nt in size, contains 12 ORFs (13 genes), and has a structural organization differing from that of other sequenced GLRaVs. Its strategy of replication conforms to that of other closterovirids [e.g. *Beet yellows virus* (BYV) and *Citrus tristeza virus* (CTV)] encompassing the direct translation of the 5' terminal ORF1A and 1B and the translation of the the downstream ORFs via a set of a eleven 3' co-terminal subgenomic RNAs. GLRaV-1 genome is 18,659 nts in size and comprises 9 ORFs (10 genes). It has the peculiar characteristic of a double minor coat protein gene. The genome of GLRaV-4 is the smallest of all (13,700 nts, 6 ORFs, 7 genes) and apparently lacks the minor coat protein gene. GLRaVs differ in various vays (molecularly, biologically, ultrastructurally, and epidemiologically) from most of the known closteroviruses, with none of which they are serologically related. GLRaVs were also thought to be serologically distinct from one another until a distant serological relationship was found between GLRaV-1 and GLRaV-3 using monoclonal antibodies raised to GLRaV-1. Regardless of the genus to which they belong, GLRaVs show sequence variations that give rise to a population of molecularly distinguishable strains that are arranged into groups. In general, GLRaV-1 and GLRaV-3 are strong leafroll symptom inducers, whereas GLRaV-4 isolates are associated with mild symptoms. Some molecular variants of GLRaV-2 (e.g. GLRaV-2 RG) do not induce leafroll but are involved in severe cases of graft incompatibility. GLRaV-7 is a mild leafroll inducer (some isolates were found in symptomless vines) and differs in many ways from all the other GLRaVs, so as to be classified in a new genus denoted *Velarivirus*. The viral genome is 16,496 nts in size, and comprises 10 ORFs (11genes).

Cytopathology: A characterizing feature of all GLRaV infections is the presence of intracellular inclusions in phloem tissues made up of aggregates of virus particles intermingled with single or clustered mebranous vesicles containing finely stranded material thought to be viral RNA. Membranous vesicles can derive either from peripheral vesiculation of mitochondria followed by disruption of the organelles (GLRaV-1, GLRaV-3, one isolate of GLRaV-4) or from vesiculation of the endoplasmic reticulum (GLRaV-2 and GLRaV-7).

Transmission: Leafroll is graft-transmissible and persists in propagative material (budwood, roostocks, grafted vines) which is largely responsible for its dissemination over medium and long distances. Spread at a site is mediated by mealybug and soft scale insect vectors. Natural field spread of leafroll disease has been reported from many countries in Europe and elsewhere. GLRaV-2 is the only leafroll virus transmissible by sap inoculation to herbaceous hosts, but has no natural vectors known. Experimental transmission of leafroll disease by *Pseudococcus maritimus* was obtained in California as early as 1961 by the late Dr. L. Chiarappa, but the results of this study have never been published. Some 30 years later the vectors of individual leafroll-agents (GLRaV-1, GLRaV-3, and GLRaV-4) began to be identified. Current knowledge tells that: (i) GLRaV-1 is transmitted in nature by the pseudococcid mealybugs *Heliococcus bohemicus*, *Phenacoccus aceris*, *Pseudococcus affinis*, *Ps.calceolariae*, *Ps. viburni*, *Ps. maritimus*, *Ps. comstocki*, and the soft scale insects *Pulvinaria vitis*, *Parthenolecanium corni*, and *Neopulvinaria innumerabilis*; (ii) vectors of GLRaV-3 are mealybugs, i.e. *Planococcus ficus*, *Pl. citri*, *Pseudococcus longispinus*, *Ps. calceolariae*, *Ps. maritimus*, *Ps. affinis*, *Ps. viburni*, *Ps. comstocki*, *Ph. aceris*, scale insects, i.e. *Pulvinaria vitis*, *Neopulvinaria innumerabilis*, *Parthenolecanium corni*, *Coccus hesperidium*, *C. longulus*, *Saissetia* and *Parasaissetia*, and scale insects of the genus *Ceroplastes;* (iii) GLRaV-4 and several of its strains) are transmitted by *Ps. longispinus* (strain 5 and 9), *Pl. ficus* (strains 6 and 9) and *Ph. aceris* (strains 5, 6 and 9). Transmission is semipersistent with acquisition and inoculation access times of *ca.* 24 h. and does not appear to be vector-specific. A single mealybug is capable of infecting a healthy vine with GLRaV-3, a virus which is more readily transmitted by mealybugs than GLRaV-1. The repeatedly observed simultaneous transmission of GLRaV-1 and GLRaV-3 with vitiviruses (GVA, GVB, GVE) has led to the suggestion that ampeloviruses may assist in the transmission of vitiviruses. It has been recently shown, however, that GVA transmission form vines double-infected by GVA and GLRaV-3 can take place without the contemporary transfer of GLRaV-3. Leafroll is transmitted by dodder from grape to grape but not to herbaceous hosts. GLRaV-7 has no known vector. The virus, however, replicates in three different species of dodder (*Cuscuta reflexa*, *C. europea* and *C. campestris*) the first two of which were able to transmit it to *Tetragonia espansa* and *Nicotiana occidentalis.* None of the GLRaVs is known to be seed-borne.

Varietal susceptibility and sensitivity: No immune variety or rootstock is known. Symptom expression depends on the variety, climate, soil condition and probably, number and types of infecting viruses. Red-berried *V. vinifera* varieties show symptoms most clearly because of the reddening of the leaves, and some of them are used as indicators. American rootstocks are usually symptomless carriers of GLRaVs. The same applies to GLRaV-2 and GLRaV-3-infected vines of *Vitis californica* and natural *V. californica* x *V. vinifera* hybrids found in USA. GLRaV-1, however, induces a bright interveinal reddening in *Vitis coignetiae.* GLRaV-2 has been found in symptomless vines of *Muscadinia rotundifolia* and *Vitis aestivalis* in Mississippi (USA).

Geographical distribution: Worldwide

Detection: In many cases, leafroll can be detected by its symptoms in the field on red-fruited varieties. Indexing on red-fruited cultivars such as Cabernet sauvignon, Cabernet franc, Pinot noir, Merlot, or the hybrid LN 33 is still the most popular method for identifying the disease, but it does not discriminates between GLRaVs and was reported to be less sensitive than ELISA. GLRaV-2, the only member of the group to be mechanically transmissible, has a number of minor biological and molecualr variants which can be differentiated by the reaction of inoculated *Nicotiana* species and by molecular techniques. All GLRaVs can be identified by serological and nucleic acid-based techniques. Polyclonal antisera and /or monoclonal antibodies have been raised to each single GLRaV. These reagents are routinely used for ISEM, classical double antibody sandwich ELISA (chromo-ELISA) or Lumino-ELISA, and some are commercially avaliable. Leaf tissues or petioles from mature symptomatic leaves of *V. vinfera* and cortical shavings from mature dormant canes of *V. vinifera*, American *Vitis* species and rootstocks are the best antigen sources for serological assays. Composite samples should be used to minimize false negative responses that may originate from the unven distribution of GLRaVs in chronically infected vines. Foliar tissues are not recommended for serological GLRaVs detection in American *Vitis* species and roostocks. As to nucleic acid-based assays, cloned cDNA probes and riboprobes to GLRaV-1 and GLRaV-3 have been produced from denatured double-stranded RNA (dsRNA) and a number of virus-specific, broad-spectrum, and degenerate primers have been designed and successfully used for PCR (single-step, nested, multiplex, real-time, Taq-Man low density array, loop-mediated isothermal amplification of nucleic acid) detection of virtually all GLRaVs. The presence of high molecular weight double-stranded RNAs (dsRNA) in phloem tissue extracts can be used as infection marker. Disappearance of dsRNAs from vines submitted to sanitation treatments is regarded as evidence for successful virus elimination. However, dsRNAs cannot be utilized for virus identification, unless they are hybridized with virus-specific probes.

Control: Production and use of clonally selected and sanitized propagation material is very effective and the only preventive method available for leafroll control. Most leafroll agents can be eliminated from infected sources by heat therapy combined or not with *in vitro* meristem tip culture, somatic embryogenesis, electrotherapy and *in vitro*

chemotherapy with a range of different drugs. No sources of resistance are known in *V. vinifera.* Protection of healthy stocks from vector-mediated reinfection in the field is difficult. Maximizing the distance between newly established and old virus-infected vineyards reduces the rate of virus spread and rogueing of infeced vines as soon they show symptoms can help to this effect. Farm equipments should be carefully cleaned before moving between vineyards as they can assist in vector dispersal. Pesticide sprays may be useful in regional control programmes but are not very effective in controlling virus dissemination. However, insecticides with systemic properties used through the irrigation system or as a foliar spray, can kill also mealybugs sheltered under the bark or in the vine roots. Introduction of transgenic resistance to GLRaV-2 and GLRaV-3 is being attempted by engineering different viral genes into rootstocks and European grape cultivars but this work is not progressing much.

2. HISTORICAL REVIEW.

1905 **Ravaz and Roos**: Occurrence in France of "rougeau", a grapevine disorder similar to leafroll.

1906 **Arcangeli:** Occurrence in Italy of "rossore", a grapevine disorder similar to leafroll.

1924 **Ravaz ad Roos**: Detailed description of "rougeau" in France.

1935 **Scheu**: Demonstration of graft transmission of leafroll from diseased to healthy *Vitis vinifera*. Hypothesis of the viral origin of leafroll.

1936 **Scheu**: Leafroll is widespread in German vineyards.

1946 **Harmon and Snyder**: The "White Emperor" disease is graft-transmissible and is regarded a virus disease.

1954 **Hewitt**: Leafroll in California.

1958 **Goheen** *et al.*: White Emperor and leafroll are identical diseases.

1958 **Fraser:** Leafroll in Australia.

1958 **Vuittenez:** Leafroll in France

1960 **Blattny** *et al.*: Leafroll in Czechoslovakia.

1961 **Chiarappa**: Unpublished report with photographic documentation of transmission of leafroll symptoms to cv. Mission seedlings by *Ps. maritimus.*

1965 **Goheen** *et al.*: Leafroll virus can be inactivated *in vivo* by heat therapy.

1967 **Hoefert and Gifford**: Study of the effects of leafroll infection on vine anatomy

1967 **Chamberlain**: Leafroll in New Zealand.

1967 **Belli** *et al.*: Leafroll in Italy.

1968 **Bovey**: Leafroll in Switzerland.

1969 **Lehoczky** *et al.*: Leafroll in Hungary.

1970 **Dimitrijevic**: Leafroll in Yugoslavia.

1970 **Luhn and Goheen**: Leafroll found in the original grapevine stocks imported from Europe into California in 1890. The incidence if the disease was less than 20% as compared with 80 to 100% in commercial vineyards. As no apparent spread of the disease was observed, roostocks are suggested as the major source of leafroll dissemination.

1971 **Mendgen:** Presence of filamentous particles in grapevines with symptoms of flavescence dorée in West Germany. These particles are probably closteroviruses associated with leafroll.

1973 **Tanne and Nitzany**: Leafroll in Israel.

1974 **Tanne** *et al.*: Transmission of a virus to herbaceous plants from a leafroll-infected vine in Israel. Later studies showed that the virus is an occasional contaminant.

1975 **Lider** *et al.*: Studies on the effects of leafroll on yield of grapevines in California.

1975 **Martelli and Piro:** Evidence from a herbarium that leafroll occurred in Sicily in the second half of the 19th century.

1976 **Tanaka:** Leafroll in Japan.

1976 **Kliever and Lider**: Study of biochemical changes found in grapevine infected with leafroll in California.

1977 **Abracheva**: Leafroll in Bulgaria.

1979 **Namba** *et al.*: Closterovirus-like particles with an estimated length of 1000 nm found in thin sections of phloem tissue and in leaf dip preparations of leafroll-diseased grapevines in Japan. Absence of such particles in healthy grapevines. Suggestion that a closterovirus may be the agent of the disease.

1981 **Faoro** *et al.*: Aggregates of closterovirus-like particles observed in thin sections of phloem from leafroll-diseased grapevines, but not in similar praparations from healthy plants.

1981 **Sasahara** *et al.*: First record of successful elimination of leafroll in grapevine by using meristem tip culture in Japan.

1982 **Von der Brelie and Nienhaus**: Light and electron microscope study of cytopathological changes induced by leafroll in grapevines. Presence of virus-like particles in thin sections of leafroll-diseased vines, but not in healthy controls.

1982 **Barlass** *at al.:* Elimination of leafroll by *in vitro* meristem tip culture and apex fragmentation.

1983 **Castellano** *et al.*: Ultrastructural study of leafroll-infected grapevine tissues.

1983 **Woodham and Krake**: Leafroll in transmitted by dodder (*Cuscuta campestris*) to grapevines but not to herbaceous hosts.

1984 **Gugerli** *et al.*: Extraction and first purification of closterovirus-like particles with maximum particle length of 2200 nm (type I) and 1800 nm (type II) from leafroll-diseased grapevine leaves in Switzerland. Production of polyclonal antisera for use in ELISA.

1984 **Hofmann:** Symptoms of leafroll in affected clones of Pinot noir and performance in West Germany.

1984 **Corbett** *et al*: Electron microscope observations by negative staining of leaf extracts from leafroll-diseased grapevines in South Africa showed the presence of closterovirus- like particles.

1985 **Mossop** *et al.*: Closterovirus-like particles and specific dsRNA found in leafroll-diseased grapevines in New Zealand.

1986 **Rosciglione and Gugerli**: GLRaV-1 and GLRaV-2 with particles of 2200 nm and 1800 nm respectively, previously found in grapevines in Switzerland, are also present in leafroll-affected grapevines from Italy. A third closterovirus type called GLRaV-3, found in grapevines affected by leafroll.

1986 **Martelli** *et al.*: Review on the detrimental effects of viral infection on grapevine physiology.

1987 **Zee** *et al.*: Studies on the cytopathology of leafroll-diseased grapevines. Purification and serology of associated closterovirus-like particles. Antiserum against a New York isolate reacts also with GLRaV-3 from Europe.

1987 **Teliz** *et al.*: ELISA testing reveals that GLRaV-3 has an uneven distribution in grapevine tissues.

1988 **Zimmermann** *et al.*: Closterovirus-like particles purified from leafroll-diseased grapevines in France. Production of rabbit and hen antibodies to GLRaV-1 and GLRaV-3 for ELISA and ISEM.

1988 **Hu and Gonsalves**: Monoclonal antibodies produced against GLRaV-3. A large dsRNA molecule is consistently isolated from leafroll-diseased grapes.

1989 **Rosciglione and Gugerli:** GLRaV-3 is transmitted by the mealybug *Planococcus ficus*. Confirmation that GLRaV-3 and the New York closterovirus isolate cross react serologically.

1989 **Tanne** *et al.*: Transmission of GLRaV-3 from grapevine to grapevine by the mealybug *Pseudococcus longispinus* in Israel.

1989 **Téliz** *et al.*: Detection of leafroll-associated closterovirus in recently infected grapevines in New York. The virus was detected in root tissues, later in the leaves. In Mexico leafroll, stem pitting and corky bark spread rapidly. *Pseudococcus longispinus* is present on weeds around diseased vineyards.

1989 **Auger** *et al.*: Leafroll and associated closteroviruses in Chile.

1989 **Kuhn**: Leafroll in Brazil.

1989 **Li** *et al.*: Leafroll and associated closteroviruses in China.

1990 **Engelbrecht and Kasdorf**: Transmission of GLRaV-3 by *Planococcus ficus* from grapevine to grapevine in South Africa. GLRaV-1 and GLRaV-2 were not transmitted. GLRaV-2, but not GLRaV-1, was detected in *P. ficus* that fed on infected vines.

1990 **Gugerli** *et al.*: Production of monoclonal antibodies to GLRaV-1 and GLRaV-3.

1990a, b **Hu** *et al.*: Characterization of leafroll-associated closterovirus-like particles from grapevine using also monoclonal antibodies. Identification of GLRaV-4.

1990 **Walter** *et al.*: Use of green grafting for detecting virus-like diseases of grapevine. With leafroll, symptoms are obtained within 20-70 days.

1990 **Agran** *et al.*: Leafroll in Tunisia.

1990 **Azeri:** Leafroll in Turkey.

1990 **Borgo**: Serological detection of GLRaV -1 and GLRaV-3 by ELISA in extracts of leaves or wood shavings. Good results in summer with extracts of basal leaves and in autumn or winter with wood shavings macerated in buffer.

1990 **Zimmermann** *et al.*: Production and characterization of monoclonal antibodies specific to GLRaV-3.

1991 **Boscia** *et al.*: Evidence of the irregular distribution of GLRaV-3 in American rootstocks, especially those containing *V. rupestris* plasma. For reliable testing, ELISA is to be applied to cortical scrapings rather than leaf tissues.

1991 **Credi and Santucci**: GLRaV-1 and GLRaV-3 cannot be detected by direct ELISA in leaves of graft-inoculated American rootstocks, but they are easily detected in inoculated LN33 vines and in *V. vinifera* varieties used as inoculum source.

1991 **Gugerli**: Review of grapevine closteroviruses.

1991 **Gugerli** *et al.*: Further characterization of GLRaV-1 and GLRaV-3 by monoclonal antibodies. Transmission of GLRaV-3 by the mealybug *Planococcus ficus.* There is evidence that other GLRaVs are involved in leafroll etiology.

1991 **Savino** *et al.*: Comparison of heat therapy and meristem tip culture for eliminating GLRaV-3 from Italian grape varieties. Heat therapy requires very long treatments and is only 20-30% successful, whereas meristem tip culture yields up to 100% sanitation.

1991 **Walter and Zimmermann**: Further characterization of closteroviruses associated with leafroll in France. Identification of GLRaV-5. GLRaV-1, -2 and -3 are common whereas GLRaV-5 is rarely detected. Some vines indexing positive for leafroll do not react positively with any of the antisera, indicating the presence of other leafroll-associated viruses.

1991 **Faoro** *et al.*: Immunocytological detection and localization of GLRaV-1 and GLRaV-3 by immunogold labelling in grapevine thin sections.

1991 **Hu** *et al.*: Comparison of different assay methods for detecting GLRaVs : ELISA, ISEM and dsRNA analysis. ELISA is recommended for large screening, whereas the other assays are more suitable for analyzing samples that gave inconclusive results with ELISA.

1991 **Boehm and Martins:** Leafroll in Portugal.

1991 **Bondarchuk** *et al.:* Leafroll and associated closteroviruses in Moldova.

1991 **Katis** *et al*: Leafroll and associated closteroviruses in Greece.

1991 **Kassemeyer**: Detection of GLRaVs in Germany.

1991 **Milkus** *et al.*: Leafroll and associated closteroviruses in Ukraine.

1991 **Namba** *et al.*: Purification and physico-chemical characterization of a grapevine corky bark-associated virus, later identified as GLRaV-2.

1992 **Habili** *et al.*: Analysis for the presence of double-stranded RNAs can be used for assessing virus elimination following sanitation treatments.

1993 **Gugerli and Ramel:** Analysis by monolconal antibodies of a Swiss source of cv. Chasselas shows the prsence of two different GLRaV-2, denoted GLRaV-2a and GLRaV-2b.

1993 **Jordan**: In a New Zealand commercial vineyard GLRaV-3 incidence increased from 9.1% in 1988 to 93.1% in 1992.

1993 **Ioannou**: Leafroll and natural spread of associated closteroviruses in Cyprus.

1993 **Pop** *et al.*: Leafroll and associated closteroviruses in Romania.

1993 **Krake**: Characterization of leafroll disease based on symptoms shown by field-infected vines and graft-transmission tests.

1993 **Segura** *et al.*: Leafroll and associated closteroviruses in Spain.

1994a, b **Saldarelli** *et al.*: Production of radioactive and non-radioactive molecular probes to GLRaV-3 from denatured dsRNA template and their use for virus identification.

1994 **Merkuri** *et al.:* Leafroll and associated closteroviruses in Albania.

1994 **Flak and Gangl**: Leafroll and associated closteroviruses in Austria.

1994 **Tzeng** *et al.*: Leafroll in Taiwan.

1994 **Belli** *et al.*: Transmission of GLRaV-3 by the soft scale insect *Pulvinaria vitis.*

1994 **Martelli** *et al.* Leafroll and associated closteroviruses in Yemen.

1995 **Boscia** *et al.*: Revision of the nomenclature of GLRaVs and use of Arabic numerals in the species names. Former GLRaV-2 is re-named GLRaV-6.

1994 **Minafra and Hadidi**: Detection of GLRaV-3 in viruliferous mealybugs by PCR.

1995 **Castellano** *et al.*: Mechanical transmission of GLRaV-2 and ultrastructural study of infected tissues of *Nicotiana benthamiana.*

1995 **Faoro and Carzaniga**: Ustrastructural study of GLRaV-1 and GLRV-3 infections. Observation of peripherically vesiculated mitochondria.

1995 **Golino** *et al.* : Transmission of GLRaV-3 by *Pseudococcus affinis* in California.

1995 **Gozsczynski** *et al.*: Production of antisera to GLRaVs using electrophoretically separated coat protein subunits as antigens

1995 **Greif** *et al.*: Association of GLRaV-2 in Italy and France with a graft incompatibility revealed by Kober 5BB.

1996 **Haidar** *et al.*: Leafroll and associated closteroviruses in Lebanon.

1996 **Gozsczynski** *et al.:* Identification of two different mechanically transmissibile strains of GLRaV-2.

1996 **MacKenzie** *et al.*: Distribution and incidence of GLRaVs in Canadian viticultural districts.

1996 **Choueiri** *et al.*: Identification of GLRaV-7 and production of a polyclonal antiserum.

1996 **Lahogue and Boulard:** Search for genes of resistance in grapevines. None of 223 accessions of European, American, and Asian *Vitis* species inoculated by green grafting with a GLRaV-1 and GLRaV-3 sources were resistant.

1997 **Rowhani and Uyemoto**: Comparative trials between indexing and laboratory detection methods show that the latter are more sensitve for GLRaVs detection. Viruses are irregularly distributed in the vines.

1997 **Habili and Nutter**: In an Australian commercial vineyard GLRaV-3 incidence increased from 23.1% in 1986 to 51.9% in 1996. No vector was identified.

1997 **La Notte** *et al.:* Development of a spot-PCR technique for GLRaVs identification.

1997 **Gugerli** *et al.*: Serological characterization of GLRaV-6 and production of monoclonal antibodies.

1997 **Guidoni** *et al.*: Elimination of GLRaV-3 by heat therapy improves agronomic performances of a cv. Nebbiolo clone and the quality of the must.

1997 **Faoro**: Comprehensive review of the ultrastructure of GLRaVs infections. GLRaV-3 induces mitochondrial vesiculation.

1997 **Martelli** *et al.*: Comprehensive review of the properties of GLRaVs.

1997 **Cabaleiro** *et al.*: GLRaV3 is transmitted by *Planococcus citri* in a semipersistent manner.

1997 **Ling** *et al.*: Cloning an sequencing of the coat protein gene of GLRaV-3 and its expression in transgenic tobacco.

1997 **Fortusini** *et al.*: Transmission of GLRaV-1 by the soft scale insects *Parthenolecanium corni* and *Neopuvinaria innumerabilis.*

1997 **Petersen and Charles**: *Pseudococcus calceolariae* acts as vector of GLRaV-3 in New Zealand.

1998 **Al-Tamimi** *et al.*: Leafroll and associated closteroviruses in Jordan.

1998 **Alkowni** *et al.*: Leafroll and associated closteroviruses in Palestine.

1998 **Ling** *et al.*: Extensive sequencing of GLRaV-3 genome. GLRaV-3 appears to be a typical closterovirus.

1998 **Zhu** *et al.:* The sequenced genome of GLRaV-2 has the same structural organization of that of *Beet yellows virus*, the type species of the genus *Closterovirus*.

1998 **Routh** *et al.*: Use of degenerate primers for PCR detection of GLRaV-4 and GLRaV-5.

1998 **Wilcox** *et al.*: GLRaV-3 detected in native American vines in western New York State.

1998 **Saldarelli** *et al.*: Use of degenerate primers for PCR detection of GLRaV-1 and GLRaV-7.

2000 **Krastanova** *et al.*: GLRaV-2 and GLRaV-3 genes engineered in grapevine rootstocks to induce resistance.

2000 **Abou Ghanem -Sabanadzovic** *et al.*: Identification and partial characterization of a new strain of GLRaV-2.

2000 **Boscia** *et al.*: Intriguing association of GLRaV-6 with cv. Cardinal in Italy and Greece. Production of a new set of monoclonal antibodies.

2000 **Castellano** *et al.*: Ultrastructural study of GLRaV-2 and GLRV-7 infections. Demonstration that the membranous vesicles accumulating in the cytoplasm derive from proliferation of the endoplasmic reticulum.

2000 **Kim** *et al.*: Leafroll and associated closteroviruses in South Korea.

2000a **Golino** *et al.***:** Association of an unusual strain of GLRaV-2 with a graft incompatibility condition described from California as young vine decline.

2000b **Golino** *et al.*: Mealybug species *Pseudococcus longispinus*, *Ps. viburni*, *Ps. maritimus*, *Ps. affinis* and *Planococcus citri* transmit with various efficiency GLRaV-3 in California but not GLRaV-1, GLRaV-2 and GLRaV-4.

2000 **Karasev**: Review article on closteroviruses. Proposal for the establishment of *Vinvirus* (later called *Ampelovirus*), a new genus having GLRaV-3 as type species.

2000 **Fazeli and Rezaian**: Partial sequencing of GLRaV-1 genome.

2000 **Gugerli**: Detection of GLRaVs by Lumino-ELISA, a chemiluminometric enzyme-linked immuosorbent assay.

2000 **Gonsalves:** Review article on the molecular traits of GLRaVs.

2000 **Monis**: Identification of GLRaV-8 and production of monoclonal antibodies.

2000 **Ling** *et al.*: Completion of the nucleotide sequence of GLRaV-3 genome and use of the HSP90 and coat protein genes for producing transgenic rootstocks.

2000 **Meng** *et al.*: Completion of the nucleotide sequence of GLRaV-2 genome.

2000 **Digiaro** *et al.:* Survey of GLRaVs in Mediterranean and Near East countries.

2000 **Mannini and Credi**.: Evidence that vines sanitized from leafroll have superior qualitative and quantitative traits.

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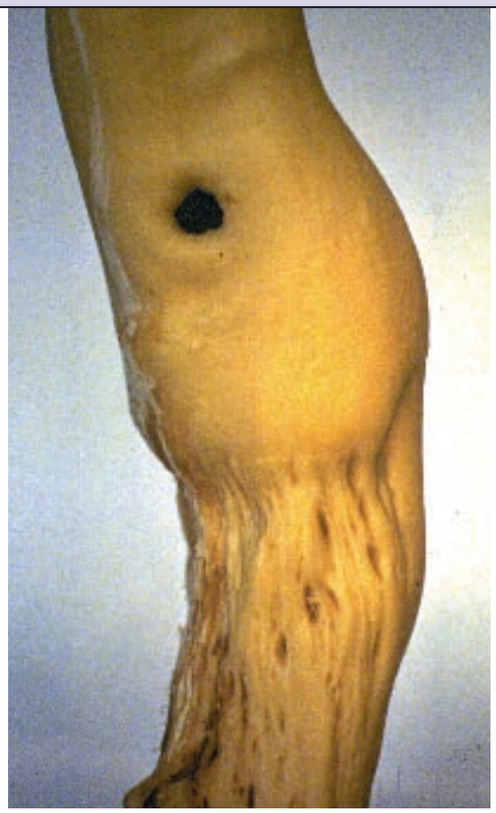
RUGOSE WOOD COMPLEX


RUGOSE WOOD COMPLEX

The rugose wood complex consists of several diseases (Grapevine rupestris stem pitting, Grapevine kober stem grooving, Grapevine corky bark, Grapevine LN33 stem grooving) that are latent in ungrafted *Vitis vinifera* and, with a few exceptions, in American *Vitis* species and rootstock hybrids, but develop in grafted vines. Woody cylinder alterations resembling rugose wood symptoms are reported in the French literature of the early 1900s as possible physiological disorders. Rugose wood was first identified and described from southern Italy in the early 1960s as a graft-transmissible disease, and was considered to be a local problem until its discovery in Hungary in 1967. Now it is known to occur worldwide.

1. DESCRIPTION.

Main synonyms: Stem pitting, stem grooving (Eng.); legno riccio (Ital.); bois strié, cannelures du tronc (Fr.); madera rizada (Sp.); lenho rugoso (Port.). Synonyms for corky bark: rough bark (Eng.); suberosi corticale (Ital.); écorce liégeuse (Fr.); Korkrindenkrankheit (Germ.).

Symptoms: Affected vines appear less vigorous than normal and may show delayed bud opening in spring. Some decline and die within a few years from planting. Grafted vines often show a swelling above the bud union and a marked difference between the relative diameter of scion and rootstock. With certain cultivars, the bark above the graft union is exceedingly thick and corky, has a spongy texture and a rough appearance, a condition known as "corky rugose wood". The woody cylinder is typically marked by pits and/or grooves which correspond to peg- and ridge-like protrusions on the cambial face of the bark. These alterations may occur on scion, rootstock or both. The severity of wood symptoms vary according to scion/stock combinations. Climatic conditions may have a bearing on symptom expression for under cool and wet climates symptoms are milder or absent. Cases of latent infection in grafted vines are not rare. By contrast, self-rooted European grapes and, sometimes, American rootstocks, can show wood alterations, though rarely. No specific symptoms are seen on the foliage, although certain cultivars show rolling, yellowing or reddening of the leaves similar to those induced by leafroll. Bunches may be fewer and smaller than normal and the crop reduced by 20-30%. The four diseases of the rugose wood complex can be recognized and sorted out by graft transmission to the indicators *Vitis rupestris*, LN 33 and Kober 5BB:

a. *Rupestris stem pitting*. Distinct basipetal pitting limited to a band extending downwards from the point of inoculation in *V. rupestris*. LN 33 and Kober 5BB remain symptomless.
b. *Corky bark*. Grooving and pitting of the entire surface of the stem of *V. rupestris* and LN 33, but no symptoms in Kober 5BB. Severe stunting of LN 33 is accompanied by rolling and reddening of the leaves and by most typical internodal swelling and craking of the canes.
c. *Kober stem grooving*. Marked grooving appear on the stem of Kober 5BB; no symptoms in *V. rupestris* and LN 33.
d. *LN 33 stem grooving*. Grooves occur on the stem of LN 33, much the same as with corky bark, but no internodal swelling of the shoots nor foliar discolorations are present. *V. rupestris* and Kober 5BB show no symptoms.

Agents: Putative agents of individual diseases of the rugose wood complex are members of the genera *Vitivirus* and *Foveavirus*, which, together the genus *Trichovirus* (two species of which are grapevine pathogens but do not seem to be involved in rugose wood aetiology) had been assigned to *Flexiviridae*, a novel family that derives its name from the flexuous aspect of its virions, which was later split in two families, *Alpha-* and *Betaflixiviridae*, the latter comprising trichoviruses, vitiviruses and foveaviruses. The chief characteristics of members of this family are: (i) flexuous filamentous virions 730 to 800 long and 12-13 nm in diameter, some showing a distinct cross banding; (ii) monopartite, positive sense, ssRNA genomes with a 3'-poly(A) tail; (iii) translation of at least some ORFs from both 5'- and 3'- coterminal subgenomic mRNAs; (iv) up to 6 open reading frames ordered from 5' to 3'; (v) an alpha-like replication protein containing conserved methyl transferase, helicase and RNA-dependent RNA polymerase (RdRp) motifs; (vi) a single coat protein (CP) 22-44 kDa in size. Vitiviruses and foveaviruses are phloem-restricted in grapevines, but whereas most vitiviruses are mechanically transmissibile to herbaceous hosts, though with difficulty, foveaviruses are not. The genome of all viruses consists of a single species of single-stranded positive sense RNA with mol. wt 2.6-3.05×10^6 that accounts for *ca.* 5% of the particle weight. Coat protein subunits have a single size and M_r of 22-28 kDa. Rugose wood-associated viruses

have a worldwide distribution. Records exist from Europe, the Mediterranean basin, Near and Far East, Australasia, South Africa, and North and South Americas.

Grapevine rupestris stem pitting-associated virus (GRSPaV), a definitive member of the genus *Foveavirus*, is the agent associated with Grapevine rupestris stem pitting disease. It is also frequently found in vines affected by "Syrah decline", but no cause-effect relationship with this disease has ultimately been established. Some isolates were shown to have a detrimental effect on the host by reducing the photosynthetic potential and increasing the dark respiration rate. Virus particles are about 730 nm in length and are not readily observed with the electron microscope. GRSPaV occurs in nature as a family of molecular variants. The collective recognition of nine divergent variants makes this virus one of the most molecularly differentiated among the grapevine-infecting viruses. Viral strains may or may not be associated with stem pitting in *V. rupestris* or with vein necrosis in the rootstock 110R, a disease which is described in detail in "Minor virus diseases". The viral genome, which has been totally sequenced, has a mol. wt of about 3.05×10^6 Da and a size of 8,726 nts. It comprises 5 or 6 ORFs encoding, in the order, the replication-associated proteins plus an AlkB and an OTU-like cystein proteinase domain (244 kDa), movement proteins [triple gene block, with a size of 25 kDa (TGBp1), 13 kDa (TGBp2) and 8 kDa (TGBp3)] and the coat protein (28 kDa), that contains a nuclear localization signal. The 6th ORF, when present, encodes a 14 kDa protein with unknown function. TGBp1 has a cytoplamic distribution and forms distinctive subcellular structures (punctate bodies). TGBp2 and TGBp3 localize to the endoplamic reticulum. The replicase protein forms intracytoplasmic globular structures (punctate bodies) that associate with the endoplamic reticulum. GRSPaV seems to be more closely related to potexviruses than carlaviruses both of which have a similar genomic organization. These relationships have evolutionary implications and suggest that GRSPaV may have evolved from an ancient recombiantion event between a carlavirus and a potexvirus in which ORF 4 and 5 but not the 3' non coding region of the carlavirus were replaced by those of the the potexvirus. A full-lenght cDNA clone of the virus has been synthesized, that replicates in the grapevine and in several experimental hosts, including *N. benthamiana*.

Grapevine virus A (GVA), the type species of the genus *Vitivirus*, is the putative agent of Grapevine kober stem grooving. It occurs as a series of molecular variants, three separate groups of which were identified in South Africa and four in Italy. Some of the variants of group II seem to be involved in the aetiology of "Shiraz disease" in South Africa and Australia. Virus particles are flexuous filaments about 800 nm long. Viral RNA has a mol. wt of about 2.6×10^6 Da and a size of 7,349 nts. The viral genome consists of 5 ORFs encoding, in the order, the replication-associated proteins (195 kDa), a 20 kDa protein with unknown function, the movement protein (31 kDa) that localizes to plasmodemata and induces tubule-like structures, the coat protein (22 kDa), a 10 kDa product which has nucleotide binding properties and is a pathogenicity factor and a RNA silencing suppressor. Like other vitiviruses the replication-associated protein encoded by ORF1 possesses an AlkB domain but not the motifs of a papain-like (P-pro) or ovarian tumor (OTU)-like protease domain. Minor biological and serological variants of the virus are known. An infectious cDNA clone has been produced. It was utilized for the functional and genomic analysis of the virus and was engineered into a vector for the expression of foreign proteins in herbaceous hosts and grapevines. A novel virus-induced grapevine protein (VIGG) correlated with fruit quality identified in GVA-infected vines is thought to be elicited by GVA infections.

Grapevine virus B (GVB) is a vitivirus distantly related serologically to GVA and one of the aetiological agents associated with Grapevine corky bark. GVB is also involved in young grapevine decline, a graft incompatibility condition recorded from California. Its totally sequenced RNA has a mol. wt of about 2.7×10^6 Da, a size of 7,599 nts and the same gene sequence and structural organization as GVA. This virus occurs in nature as a family of molecular variants, but biological variants are also known, two groups of which can be differentiated by the reaction of herbaceous hosts. Virus particles coated by both GVA and GVB coat protein occur in cells infected contemporarily by both viruses (phenotypic mixing). A stable full-length GVB clone was constructed and found to be infectious in *N. benthamiana.*

Grapevine virus C (GVC), a poorly characterized virus reported from Canada, was serologically unrelated to GVA and GVB and had particles with a vitivirus morphology and an estimated length of about 725 nm. GVC was classified as a separate vitivirus until it was shown to be a misindentified isolate of GLRaV-2 and was deleted from the list of valid virus species.

Grapevine virus D (GVD), a vitivirus distantly related serologically to GVA and GVB is associated with corky rugose wood, a field syndrome characterized by the presence of a striking corky condition of affected vines, just above the graft union. Virus particles are flexuous filaments about 825 nm long. The viral genome, which was sequenced only in part, has an estimated size of *ca.* 7,600 nts and a 3' terminus structurally comparable to that of GVA and GBV. Divergent molecular variants are common. Two of them from South Africa denoted GVB 935-1 and GVB-H1 were consistently recovered from corky bark-affected and corky bark-negative vines, respectively.

Grapevine virus E (GVE), a vitivirus serologically distinct from GVA and GVB, was first isolated in 2008 from the Japanese table grape cvs Aki Queen and Pione (*Vitis labrusca*) and partially characterized. Although one of the vines infected by GVE had stem pitting symptoms, no relationship between this virus and the disease could be established. GVE is a single-stranded, positive-sense RNA virus with a genome organization typical of that of members of the genus *Vitivirus*, with which it is phylogenetically related. The partial sequence of two Japanese viral isolates and the complete sequence of a South African and a North American isolate have been determined. The virus has also been found in China. The genome is 7,565-7, 568 nts in length and consists of five ORFs encoding, in the order, the replication associated proteins, a product with an unknown function, the movement protein, the coat protein and a putative silencing suppressor. A peculiar feature of the GVE genome is the presence of the AlkB domain within the helicase domain in ORF1. Contrary to other vitiviruses, GVE cannot apparently be transmitted by mechanical inoculation to herbaceous hosts.

Grapevine virus F (GVF), a novel member of the genus *Vitivirus* found in California in a grapevine accession denoted AUD46129. It induces graft incompatibility in cv. Cabernet sauvignon grafted on different rootstocks. The virus has a single-stranded RNA genome 7,551 nts in size, comprising five ORFs with a vitivirus-like oganization encoding: (i) ORF1, replication-associated proteins (1,727 aa, 197 kDa); (ii) ORF2, 20 kDa protein with unknown function; (iii) 30 kDa movement protein; (iv) 22 kDa coat protein; (v) 12 kDa protein with RNA binding properties.

Molecular properties of grapevine-infecting vitiviruses

Virus	Genome size (nt)	ORF1 (kDa)	ORF2 (kDa)	ORF3 (kDa)	ORF4 (kDa)	ORF5 (kDa)	Accession Nos.
GVA	7,351	194	20	31	22	10	X75433
GVB	7,599	195	20	37	22	14	X75448
GVD	936 (partial)	Not determined	Not determined	Not determined	18	11	Y07764
GVE	7,568	192	21	29	22	13	GU90312
GVF	7,551	196	20	30	22	12	JX105428

Cytopathology: Whereas no information is available on the cytopathology of GRSPaV infections, vitivirus-induced cellular modifications have been extensively studied, primarily in herbaceous hosts. Cytopathological features common to three vitiviruses (GVA, GVB and GVD) consist of: (i) virus particle aggregates of various size, forming bundles, whorls, banded bodies, stacked layers that, sometimes, fill the entire cell lumen; (ii) variously extended wall thickenings originating from deposits of callose-like substances; (iii) proliferation and accumulation of cytoplasmic membranes; (iv) vesiscular evaginations of the tonoplast protruding into the vacuole and containing finely fibrillar material resembling dsRNA. GVA and GVB movement proteins are associated with cell walls and plasmodesmata, as detected by gold immunolabelling.

Transmission: For many years after its discovery there were no records of natural spread of rugose wood in the field. GVA and GVB are now known to be transmitted from grapevine to grapevine by pseudococcid mealybugs and/or scale insects in a semipersistent manner. GVA, in particular, was the first RNA virus ever experimentally shown to be transmitted by mealybugs, the alleged vectors of DNA viruses. Vectors are the mealybugs *Planococcus citri*, *Pl. ficus*, *Pseudococcus longispinus*, *Ps. affinis*, *Heliococcus bohemicus*, *Phenacoccus aceris* and the scale insect *Neopulvinaria innumerabilis.* GVB is transmitted by *Ps. longispinus*, *Ps. affinis*, *Pl. ficus* and *Ph. aceris* and GVE is transmitted by *Pseudococcus comstocki.* With GVA, the first instar larvae are the most efficient vectors The simultaneous transmission of GVA, GVB and GVE with GRLaV-1 and/or GLRaV-3 had led to the suggestion that the transmission of vitiviruses is assisted by the ampeloviruses present in the same vine. GRSPaV has no known vectors, but is suspected to be pollen-borne. There are, however, conflicting reports on its presence within seed and no evidence that it occurs in seedlings from infected vines. None of the putative agents of rugose wood has alternative hosts in nature and, because of the relatively limited range of vector movement, is not disseminated over long distances by natural means. Transport of infected propagative material represents the major means of dispersal. The presence of rugose wood and its causal agents in phylloxera-free countries with a millenial history of own-rooted grapevine cultivation, suggests that the disease originated in the Old World and was distributed worldwide by commercial trading and planting of infected grafted plants.

Varietal susceptibility: Most if not all *V.vinifera* varieties and American rootstocks are susceptible. Although customarily grapevines are infected symptomlessly when ungrafted, rugose wood symptoms have been observed in self-rooted cultivars and ungrafted roostock stocks (*V. rupestris* and Kober 5BB). Latent infection can occur also in grafted vines. The intensity of wood abnormalities (pitting and grooving) vary, possibly in relation with the scion/stock combination and climatic conditions.

Geographical distribution: Worldwide

Detection: Indexing on indicators (*V. rupestris*, Kober 5BB and LN 33) is the only reliable method for detecting and sorting out the diseases of the complex. Recently, experimental evidence has been obtained of the very close association of some strains of GRSPaV, the putative agent of rupestris stem pitting, with the "vein necrosis" condition shown by trhe rootstock 110R. Most vitiviruses, but not foveaviruses, are mechanically transmissible, though with difficulty, to a restricted range of herbaceous hosts (mostly *Nicotiana* species). Individual viruses can be identified by ELISA or dot immunobinding on nylon membranes using polyclonal antisera and/or monoclonal antibodies, when available. The best antigen sources for serological diagnosis are cortical shavings from mature dormant canes. Additional assays include: single step or nested RT-PCR, immunocapture RT-PCR, spot-RT-PCR , and real time RT-PCR using degenerate or virus-specific primers. Immuno-capture RT-PCR is 1000-fold more sensitive than ELISA for virus detection in grapevines.

Control: Use for propagation of virus-free scionwood and rootstocks obtained by sanitary selection combined with sanitation is of paramount importance to avoid introduction of infected vines in the vineyards. However, since symptomless infections does not make sanitary selection totally reliable, all sources must be indexed and/or laboratory tested. In general, rugose wood agents can be eliminated with reasonable efficiency by heat therapy, meristem tip culture, or a combination of the two. GVA can be eliminated to a very hight rate (up to 97%) by the procedure used for cryopreservation of grapevine shoot tips and up to 100% by somatic embryogenesis, the same as GRSPaV. Efficient sanitation techniques are also *in vitro* meristem tip culture combined heat therapy and/or chemotherapy. Control of mealybugs is difficult for they overwinter under the bark of grapevines and possess an unwettable waxy covering. Thus, no efficient strategy has yet been developed for the chemical control of vectors. In general, though, the same control strategy being developed for leafroll disease should be applicable to the rugose wood syndromes induced by vitiviruses. No natural sources of resistance to any of the rugose wood agents are known but the possibility of using pathogen-derived resistance in *Vitis* is being explored. Using a *Nicotiana benthamiana* model system, several resistant plant lines were obtained by transformation with the coat protein and the movement protein genes of GVA and GVB. Transgene expression was detected in these plants and in transformed grapevine explants.

2. HISTORICAL REVIEW.

Names like "legno riccio", "stem pitting" and "stem grooving", if not otherwise associated with a specific syndrome, are synonymized with "rugose wood".

1954 **Hewitt**: Rough bark, a virus-like disease, described from California.

1961 **Graniti and Ciccarone**: First record of rugose wood from southern Italy.

1962 **Hewitt** *et al.*: Graft transmission of rough bark to LN 33. Name of the disease changed into corky bark.

1963 **Goidanich and Canova**: First record of corky bark in Europe.

1963 **Faccioli**: First histological study of corky bark-affected grapevines.

1964 **Graniti**: Detailed description of rugose wood symptoms. Suggestion that it may be caused by a virus.

1965 **Graniti and Martelli**: Demonstration of the infectious nature of rugose wood. Histological study of diseased vines. Suggestion that rugose wood may be a disease of combination requiring the contact of scion and rootstock for the development of symptoms, and that it may be a composite disease resulting from the interaction of different viruses among which GFLV.

1965 **Beukman and Goheen**: Brief account of the histological modifications of corky bark-affected LN 33.

1965 **Goheen** *et al.*: Corky bark is remarkably heat stable and difficult to eliminate by heat therapy.

1967 **Martelli** *et al.*: First record of rugose wood outside of Italy (Hungary).

1968 **Lehoczky** *et al.*: Observation of rugose wood symptoms in self-rooted vines. Rugose wood may not require a grafted plant for full symptom expression.

1968 **Goheen**: Evidence that corky bark and leafroll, despite similarities in the symptoms on the foliage are different diseases. At 38°C the minimum inactivation period for leafroll is 56 days and for corky bark 98 days.

1968 **Hewitt**: Up-to-date review on grapevine virus and virus-like disease worldwide. First record of rugose wood symptoms outside of Europe (Israel).

1969 **Beukman and Gifford**: Detailed account of adverse effects of corky bark on the anatomy of *Vitis*.

1970 **Beukman and Goheen**: Up-to-date review of corky bark.

1970 **Graniti and Martelli**: Up-to-date review of rugose wood.

1971 **Hewitt and Neja**: Rugose wood in California (USA).

1971 **Engelbrecht and Nel**: Rugose wood and fanleaf are not related, based on graft transmission tests.

1972 **Lehoczky**: Destructive effects of rugose wood registered in Hungary in both self-rooted and grafted European grape varieties.

1973 **Bovey and Brugger**: Further evidence that GFLV may not be implicated in the etiology of rugose wood in Switzerland.

1973 **Goheen and Luhn**: Heat treatment of dormant buds grafted onto LN 33 is effective against corky bark.

1975 **Castillo** *et al.*: Green grafting useful for corky bark indexing.

1975 **Hewitt**: Successful graft transmission of Californian rugose wood.

1977 **Mink and Parsons**: Use of growth chambers for rapid symptom expression of corky bark in *Vitis* indicators.

1978 **Goheen and Luhn**: Suggestion that corky bark and rugose wood are the same disease. No nepoviruses implicated in their aetiology.

1979 **Legin** *et al.*: Heat therapy effective against rugose wood.

1979 **Anonymous**: A review of rugose wood in Italy.

1980 **Conti** *et al.*: Recovery by mechanical inoculation of a closterovirus with particles 800 nm long, from a rugose wood-infected vine. Virus provisionally called grapevine stem pitting-associated virus (GSPaV).

1980 **Teliz** *et al.* a,b,c: A series of three papers reporting the occurrence and field spread of corky bark in Mexico and evaluating symptoms induced by natural infections of corky bark in formerly virus-free self-rooted or grafted European grape varieties and rootstocks.

1981 **Boccardo and D'Aquilio**: Physicochemical characterization of GSPaV.

1981 **Abracheva**: Survey of over 650 grapevine cultivars and hybrids for rugose wood reaction in Bulgaria.

1982 **Sarooshi** *et al.*: Rugose wood in Australia.

1983 **Rosciglione** *et al.*: First experimental evidence that a RNA virus (GVA), is transmitted by a pseudococcid mealybug (*Pseudococcus longispinus*).

1984 **Milne** *et al.*: Evidence that GSPaV can occur in grapevines together with another similar but serologically unrelated virus with short closterovirus-like particles, denoted Grapevine virus B (GVB). GSPaV re-named Grapevine virus A (GVA).

1985 **Rosciglione and Castellano**: Demonstration that GVA is transmitted also by *Planococcus citri* and *P. ficus*.

1985 **Prudencio**: M. Sc. thesis describing rupestris stem pitting disease in comparison with corky bark.

1985 **Corbett and Wiid**: Closterovirus-like particles found in extracts from vines affected by corky bark and rugose wood in South Africa.

1985 **Garau** *et al.*: Assessment of crop losses induced by rugose wood to two different European grape varieties.

1985a **Savino** *et al.*: Experimental confirmation that rugose wood may not express symptoms in grafted indicators. Rugose wood and corky bark are not the same disease.

1985b **Savino** *et al.*: Evaluation of the effect of rugose wood on cv. Italia propagated on six different rootstocks.

1985 **Gallitelli** *et al.*: Application of spot hybridization for the detection of GVA in grapevine sap.

1985 **Castrovilli and Gallitelli**: Physicochemical comparison of two Italian isolates of GVA.

1985 **Murant** *et al.*: Heracleum latent virus and GVA are distantly serologically related.

1987 **Kuniyuki and Costa**: Rugose wood in Brazil

1988 **Goheen**: First published description of rupestris stem pitting.

1989 **Savino** *et al.*: Experimental confirmation of the complex nature of rugose wood based on the differential reaction of woody indicators. First report of Kober stem grooving.

1989 **Li** *et al.*: Rugose wood in China.

1989 **Martelli**: Rugose wood recorded in southern Mediterranean and Arab countries.

1989 **Garau** *et al.*: First indication of the possible existence of LN 33 stem grooving, an additional disease of the rugose wood complex.

1989 **Monette** *et al.*: A low molecular weight dsRNA associated with rupestris stem pitting.

1989 **Tanne** *et al.*: Transmission of corky bark by the mealybug *Planococcus ficus*.

1990 **Monette and James**: Detection of two biologically distinct but serologically indistinguishable isolates of GVA.

1990 **Engelbrecht and Kadsorf**: Natural field spread of corky bark in South Africa associated with the presence of *Planococcus ficus*.

1991 **Engelbrecht** *et al.*: Three types of wood disorders of the stem-grooving type observed in South African grapevines, similar to Kober stem grooving, Corky bark and Rupestris stem pitting. The first two disorders appear to be spreading in the vineyards.

1991 **Azzam** *et al.*: Two distinct dsRNAs with a mol. wt of 5.3 and 4.4×10^6 associated with rupestris stem pitting in grapevines from California and Canada. Similar dsRNA species were detected, but not consistently in grapevines from New York. Suggestion that the disease is not related to closteroviruses associated with grapevine leafroll and corky bark. No

closterovirus-like particles found in vines affeced by rupestris stem pitting.

1991 **Gugerli** *et al.*: Presence of two distinct serotypes of GVA, both associated with a stem pitting condition of grapevines rather than with leafroll.

1991 **Namba** *et al.*: A closterovirus with particles 1440-2000 nm long serologically unrelated to all other known grapevine closteroviruses found in corky bark-affected vines. Virus later identified as Grapevine leafroll-associated virus 2.

1991 **Tanne and Meir**: A dsRNA with a molecular weight higher than 14 kDa identified in extracts from corky bark-affected vines.

1991 **Garau** *et al.*: Contemporary occurrence of Rupestris stem pitting and Kober stem grooving in symptomless scions of cv. Torbato in Italy.

1991 **Monette and James**: A closterovirus with short particles (725 nm) isolated from a corky bark-affected vine induces necrotic local lesions and systemic symptoms in *Nicotiana benthamiana.*

1991 **Minafra** *et al.* Synthesis of a cloned probe for GVA.

1991 **Saric and Korosec-Koruza**: Rugose wood recorded from Croatia and Slovenia.

1991 **Ioannou:** Rugose wood in Cyprus.

1991 **Boulila** *et al.*: Rugose wood in Tunisia.

1991 **Milkus** *et al.*: Rugose wood in Ukraine.

1992 **Boscia** *et al.*: Production of monoclonal antibodies to GVA and their use for ELISA detection of the virus in infected vines.

1992 **Martelli** *et al.*: Rugose wood in Malta.

1993 **Monette and Godkin**: Recovery of a closterovirus-like virus by mechanical inoculation from a corky bark-affected vine. Virus named Grapevine virus C (GVC).

1993 **Padilla**: Rugose wood in Spain.

1993 **Boscia** *et al.*: Purification and properties of GVB. Virus transmission by the mealybug *Planococcus ficus* induced corky bark symptoms in LN 33.

1993 **Saldarelli** *et al.*: Development and diagnostic use of a cloned probe to GVB.

1994 **Minafra** *et al.*: Sequence of the 3' end of GVA and GVB genome. Both viruses qualify of the inclusion in the genus *Trichovirus.*

1994 **Merkuri** *et al.*: Rugose wood in Albania.

1994 **Garau** *et al.*: GVA and Kober stem grooving are closely associated. Suggestion that GVA may be the causal agent of the disease.

1994 **Martelli** *et al.*: Rugose wood in Yemen in own rooted table grape vines.

1994 **Digiaro** *et al.*: Clear-cut connection of GVA and rugose wood. Suggestion that GVA is implicated in the aetiology of the disease.

1994 **Saldarelli** *et al.*: Development of digoxigenin-labelled riboprobes for the detection of GVA and GVB in infected tissue extracts.

1994 **Minafra and Hadidi**: Detection of GVA and GVB in viruliferous mealybugs by PCR.

1994 **Boscia** *et al.* Thorough comparative study of nine GVB isolates from different countries.

1995 **Chavez and Varon de Agudelo**: Rugose wood in Colombia.

1995 **Monette and Godkin**: Detection of non mechanically transmissible capillovirus-like particles in a grapevine affected by rugose wood. Since particle size (600-700 nm in length) is compatible with that of Grapevine rupestris stem pitting-associated virus (GRSPaV) particles identified in 2003, this may be the first visualization of GRSPaV.

1995 **Chevalier** *et al.*: Consistent detection of GVA in Kober stem grooving-infected grapevines by immunocapture-polymerase chain reaction. Further support of the cause-effect relationship between GVA and this disease.

1995 **Boscia** *et al.*: Rugose wood in Jordan.

1995 **Garau** *et al.*: GVA and GVB are transmitted by *Pseudococcus affinis.*

1996 **Bonavia** *et al.*: GVB is consistently associated with corky bark and is present, though not consistently, in vines showing a syndrome denoted "corky rugose wood". Efficient detection method based on TAS-ELISA developed

1996 **Saldarelli** *et al.*: Nucleotide sequence of GVB genome.

1996 **Haidar** *et al.*: Rugose wood in Lebanon.

1996 **Tanne** *et al.*: A study of the spatial distribution pattern of corky bark in a cv. Thompson seedless vineyard in Israel. Suggestion that spreading is by a vector that transmits in a semipersistent manner.

1996 **Goszczynski** *et al.*: GVA and GVB are serologically related.

1997 **Choueiri** *et al.*: GVA and GVD are serologically distantly related.

1997 **Boscia** *et al.*: Review of the properties of putative grapevine-infecting trichoviruses (GVA, GVB, GVC, and GVD) later assigned to the genus *Vitivirus.*

1997 **Faoro:** Review of the cytopathology of grapevine trichovirus infections.

1997 **Abou Ghanem** *et al.*: Description of Grapevine virus D (GVD).

1997a **La Notte** *et al.*: Experimental evidence that GVA is transmitted by *Ps. longispinus* in a semi-persistent manner.

1997b **La Notte** *et al.*: Development of a PCR technique for the detection of GVA and GVB in nylon membrane-spotted sap.

1997 **Minafra** *et al.*: Nucleotide sequence of GVA genome and taxonomic position of the virus.

1997 **Martelli** *et al.*: Establishment of the genus *Vitivirus* with GVA as type species. GVA, GVB, and GVD removed from the genus *Trichovirus* and assigned to the new genus.

1997 **Rubinson** *et al.*: Antiserum to the movement protein of GVA is useful for virus detection in ELISA.

1997 **Guidoni** *et al.*: Elimination of GVA from cv. Nebbiolo clones by heat therapy improves agronomic performance of the vines and quality of the must.

1998 **Meng** *et al.*: Sequence and structrural organization of *Grapevine rupestris stem pitting-associated virus* (GRSPaV) genome.

1998 **Zhang** *et al.*: Sequencing of a Californian isolate of GRSPaV. The virus is not seed-borne.

1998 **Martelli and Jelkmann**: Establishment of the genus *Foveavirus.* GRSPaV is assigned to this genus.

1998 **Alkowni** *et al*: Rugose wood in Palestine.

1999 **Meng** *et al.*: Consistent association of GRSPaV with vines indexing positive for Rupestris stem pitting. Further support to the cause-effect relationship of GRSPaV with this disease.

1999 **Galikparov** *et al.*: Production of an infectious RNA transcript from a full-length cDNA clone of GVA.

2000a **Saldarelli** *et al.*: Movement proteins of GVA and GVB detected by gold immunolabelling in association with cell walls and plasmodemata of infected cells. GVA movement protein is also present in great quantity in the cytoplasm, intermingled with virus particle aggregates.

2000b **Saldarelli** *et al.*: Synthesis of full-length cDNA copies of GVA and GVB genomes.

2000 **Minafra** *et al.*: Production of a polyclonal antiserum to a recombinant coat protein of GRSPaV and its use in dot immunobinding on polyvinyl difluoride membranes for virus detection in grapevine tissue extracts.

2000 **Martinelli** *et al.*: *Nicotiana* spp. and grapevines transformed with the movement protein genes of GVA and GVB.

2000 **Radian-Sade** *et al.*: Successful transformation of *Nicotiana benthamiana* and grapevines with the CP gene of GVA.

2001 **Buzkan** *et al.*: One-sided phenotyping mixing, i.e. GVA coat protein encapsidating GVB RNA occurs in *Nicotiana* plants doubly infected with GVA and GVB.

2001 **Boscia** *et al.*: Production of monoclonal antibodies to GVB. Confirmation of the cause-effect relationship between GVA and Kober stem grooving, GVB and Corky bark and GRSaV and Rupestris stem pitting.

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GRAFT INCOMPATIBILITY

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Infection by phloem-limited viruses may damage grapevines in the nursery (reduced graft take) or in the early stages of growth in the field (graft incompatibility). This latter condition has been known for a long time and occurs also in rugose wood-affected vines. However, the increased use of clonal material is disclosing unprecedented conditions of generalized decline that develop dramatically in certain scion-rootstock combinations, so as to represent veritable emerging diseases.

1. DESCRIPTION

Main synonyms: Incompatibilité au greffage (Fr.), incompatibilità d'innesto (Ital.)

Symptoms: Newly planted vines grow weakly, shoots are short, leaves are small-sized, with margins more or less extensively rolled downwards, and the vegetation is stunted The canopy shows autumn colours off season so that leaves turn reddish in red-berried varieties or yellow in white-berried varieties much earlier than normal. A prominent swelling forms at the scion/roostock junction and variously extended necrotic lesions may develop on the rootstock stem, which are usually not accompanied by wood abnormalities (pitting or grooving). Severely affected vines decline and may die within one or two years. Cases of graft union disorders have been observed in Europe (Kober 5BB incompatibility), California, New Zealand, Australia and Chile (young vine decline), and again California (rootstock stem lesions, grapevine necrotic union). A transitory form of incompatibility was reported from Italy under the name of bushy stunt. In this case, scions show a stunted and bushy vegetation due to the contemporary proliferation of apical and axillary buds, but the colour of the canopy remains green. Normal growth resumes with the second or third leaf, but the yield is reduced. The putative agent of bushy stunt was consistenly found in clones of the rootstock 140R in which it is latent. Syrah decline is a severe disease occurring in all countries where certain clones of cv. Syrah are grown. Foliar and trunk symptoms resemble very much those induced by rugose wood/graft incompatibililty and are shown by aged as well as young (4-year-old) vines. The nature of this disease has not been ascertained but one or more graft-transmissibile agents may be involved in its aetiology. Incompatibility may also develop in the form of a brown line of necrotic tissues at the bud union when grape cultivars hypersensitively resistant to the nepovirus ToRSV are grafted on susceptible rootstocks.

Agents: An ordinary strain of *Grapevine leafroll-associated virus 2* (GLRaV-2) is consistently associated with Kober 5BB incompatibility (Europe), and together with *Grapevine virus B* (GVB), appears to be involved in California's young vine decline. The same virus was detected in diseased Chilean grapes, though not consistently and, consistently, in Argentine grapes. A virus originally detected in cv. Redglobe in California called Grapevine rootstock stem lesion-associated virus (GRSLaV) proved to be a molecular and biological variant of GLRaV-2 (GLRaV-2 RG). Other molecular variants of GLRaV-2 were reported from New Zealand (Alphie virus), Chile, and Australia in association with young vine decline conditions. Based on the differential responses of a panel of 18 rootstocks, up to five different graft-transmissible agents inducing incompatibility could be differentiated in California. Of these, only GLRaV-2 RG was identified. The heat-labile graft-transmissible agent present in the hybrid 140R, associated with grapevine bushy stunt is still unidentified.

Transmission: GLRaV-2, a member of the genus *Closterovirus*, is not transmitted by mealybugs and does not have a known vector. Infected propagative material is to be blamed for its dissemination. GVB is mealybug-borne and can be spread at a site by these insects.

Varietal susceptibility: Appearance of graft union disorders depends more on the rootstock rather than the scion. European grape varieties grafted on tolerant rootstocks (e.g. Freedom, Harmony, Salt creek , 03916, 101-14) exhibit a green canopy and perform rather well, whereas varieties grafted on susceptible roostocks (e.g. Kober 5BB, 5C, 1103P, 3309) develop a discolored canopy, decline and may die.

Geographical distribution: Undetermined, but this type of disorders has been reported from several major grapevine-growing countries of the world.

Detection: Indexing on Caberent sauvignon is a reliable method for detecting incompatibility conditions. Known viruses associated with this disorder (different GLRaV-2 strains and GVB) can be identified by ELISA

using polyclonal antisera and/or monoclonal antibodies The best antigen sources for serological diagnosis are cortical shavings from mature dormant canes. Other assays include nucleic acid-based tecniques such as single step or nested reverse transcription-polymerase chain reaction (RT-PCR) and immunocapture RT-PCR, using degenerate or virus-specific primers.

Control: Prevent introduction of infected vines in the vineyard by using certified grafted plants or virus-free scionwood and rootstocks. Currently known graft incompatibility agents can be eliminated with reasonable efficiency by heat therapy, meristem tip culture, or a combination of the two. If scionwood is infected, the use of sensitive rootstocks is to be avoided and, whenever feasible, utilization of tolerant roostocks is advisable. Strategies on how to protect healthy stocks from vector-mediated GVB reinfection in the field are yet to be developed.

2. HISTORICAL REVIEW

1942 **Jacob**: Description of graft incompatibility in different scion/stock combinations.

1950 **Boubals and Huglin**: Report on graft incompatibility of certain varieties grafted on 57R.

1973, 1977 **Durquety** *et al.*: Two papers describing incompatibility phenomena between clonally selected accessions of different cultivars grafted on Kober 5BB.

1979 **Fallot** *et al.*: Third paper of a series on incompatibility on Kober 5BB. Graft-transmission of the incompatibility factor.

1986 **Legin and Walter**: The graft-transmissibile agent that causes incompatibility of different varieties on Kober 5BB is a virus which can be eliminated by heat treatment at 37°C for 58 days.

1991 **Savino** *et al.*: Description of bushy stunt and evidence that it is caused by a graft-transmissibile heat-sensitive agent carried by some clonal rootstocks.

1995 **Greif** *et al.*: GLRaV-2 is the cause of a graft incompatibility revealed by Kober 5BB.

2000 **Golino** *et al.*: GLRaV-2 and GVB are consistently associated with young vine decline in California.

2000 **Boubals**: Report of a national French study group investigating the aetiology of Syrah decline. No conclusion are drawn.

2000 **Boubals:** Syrah decline occurs in Argentina.

2001 **Uyemoto** *et al.*: Identification of an apparently new closterovirus denoted Grapevine rootstock stem lesion virus (GRSLV) causing stem necrosis of rootstocks, decline, and death of the vines. GRSLV has about 75% nucleotide homology with GLRaV-2.

2003 **Uyemoto and Rowhani:** Indexing on 18 different grape rootstocks reveals the existence of at least five different agents causing graft incompatibility.

2003 **Bonfiglioli** *et al.*: Report of a new molecular variant of GLRaV-2 from New Zealand.

2003 **Prodan** *et al.*: GLRaV-2 is associated, though not consistently, with a decline condition of young Thomposn seedless vines in Chile.

2003 **Gomez Talquenca** *et al*: GLRaV-2 is consistently associated with declining Cabernet sauvignon vines grafted on different roostocks in Argentina.

2003 **Martelli**: GRSLV and GLRaV-2 are serologically related and are both recognized by a panel of 18 monoclonal antibodies. Suggestion that they are molecular variants of the same virus species. GRSLV re-named Redglobe strain of GLRaV-2.

2003 **Renault Spilmont** *et al.*: Updated report on the state of the art of investigations carried out in France on Syrah decline. The problem is very complex and may involve several still unidentified factors.

2004 **Bertazzon and Angelini**: Comparison of several detection methods for the broad or specific identification of *Grapevine leafroll-associated virus 2* variants.

2012 **Al Rwahnih** *et al.*: Description of grapevine necrotic union, a graft incompatibility condition found in California. Undetermined agent.

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Boubals D., 2000. Le dépérissement de la Syrah. Compte-rendu de la réunion du Groupe de Travail National. *Progrés Agricole et Viticole* **117:** 137-141.

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Golino D.A, Sim S., Rowhani A., 2000. Identification of the latent viruses associated with young vine decline in California. *Extended Abstracts 13th Meeting of ICVG, Adelaide, Australia*: 85-86.

Gomez Talquenca G.S., Gracia O., Garcia Lampasona S., Grau O., 2003. A young grafted vine decline syndrome in Argentina vineyards. *Extended Abstracts 14th Meeting of ICVG, Locorotondo, Italy*: 85-86.

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FLECK COMPLEX

FLECK COMPLEX

The fleck complex consists of several diseases (grapevine fleck, grapevine asteroid mosaic, grapevine rupestris necrosis, and grapevine rupestris vein feathering) and viruses (Grapevine redglobe virus) that cause latent or semi-latent infections in *Vitis vinifera* and most American *Vitis* species and rootstock hybrids. Although the elusive nature of the complex hinders the assessment of its economic impact, adverse influence on vigour, rooting ability of rootstocks and on graft take has been reported.

1. DESCRIPTION.

Main synonyms:

A. Grapevine fleck: Marbrure (Fr.), maculatura infettiva, screziatura (Ital.), Marmorierung der Rebe (Germ.).

B. Grapevine asteroid mosaic: Mosaïque étoilée (Fr.), mosaico stellare (Ital.), Sternmosaik der Rebe (Germ.).

SYMPTOMS:

A. *Fleck.* The disease is latent in European grapevine varieties and in most American rootstocks. Symptoms are expressed in *Vitis rupestris* and consist of clearing of the veins of third and fourth order, producing localized translucent spots. Leaves with intense flecking are wrinkled, twisted and may curl upward. Severe strains induce also varying degrees of stunting. Fleck is an ubiquitous disease reported from most viticultural countries in the world.

B. *Asteroid mosaic.* In *V. vinifera*, leaf symptoms are characterized by star-shaped chlorotic spots, sometimes with necrotic center, irregularly distributed over the leaf blade. Leaves are asymmetric, twisted and puckered along the veins. Affected vines are often stunted, and produce little or no fruit. Leaf symptoms usually become less severe in summer. In *V. rupestris*, which is used as indicator, the disease elicits creamy-yellow bands developing along the major veins of the leaves, which are twisted and asymmetric. Asteroid mosaic symptoms have been observed in several varieties of *V. vinifera* in California. Records from Italy and South Africa have not been confirmed experimentally and a record from Greece was proven to refer to Grapevine rupestris vein feathering. The putative causal agent of the disease has only been found in California.

C. *Rupestris necrosis.* This disease, reported only from Japan, is latent in European grapevine varieties. *V. rupestris* reacts with localized necrosis of the shoots, leaf petioles and veinlets.

D. *Rupestris vein feathering.* Mild asteroid mosaic-like symptoms are shown by some European grapevine varieties (e.g. Sultanina). Transient mild chlorotic discolourations of the primary and secondary leaf veins develop in *V. rupestris* following graft inoculation. The putative causal agent of the disease so far has been found in Greece, Italy and California.

E. Grapevine red globe virus (GRGV) is *a Grapevine fleck virus* (GFkV)-like virus which apparently does not induce symptoms in European grapevine varieties (e.g. Red globe) nor in *V. rupestris*. Recorded from California and Italy, but it is likely to occur elsewhere.

Agents: All viruses of the complex, GFkV, GRGV, Grapevine asteroid mosaic-associated virus (GAMaV), and Grapevine rupestris vein feathering virus (GRVFV) are all phloem-limited and non mechanically transmissible. All have isometric particles about 30 nm in diameter with rounded contour and prominent surface structure with clusters of coat protein subunits arranged as pentamers and hexamers. GFkV particles sediment as two centrifugal components, T made up of empty protein shells and B, containing the genome, which is a monopartite single-stranded, capped, positive sense RNA with high cytosine content (*ca.* 50%). GFkV genomic RNA constitutes about 35% of the particle weight. The coat protein (CP) of GFkV and GRGV particles is made up of a single protein species with M_r of *ca.* 25 kDa, whereas the CP of GAMaV and GRVFV consists of a major protein of 21 kDa and a minor prtotein of 25 kDa. The complete sequence of GFkV and partial sequences of GRGV, GAMaV, and GRVFV genomes are available. GFkV genomic RNA (Mol. wt of 2.6×10^6) is 7,564 nt in size and contains four open reading frames (ORF) that encode a 215.4 kDa polypeptide with the conserved motif of replication associated proteins (ORF 1), the CP (ORF 2), and two proline rich polyproteins of 31.4 kDa (ORF 3) and 15.9 kDa (ORF 4) with unknown function. The 3' end of the GRGV genome is structurally similar to that of GFkV except for the lack of ORF 4. The genomic structure of GAMaV and GRVFV differs from the above in that both these viruses have a single ORF encoding a large polypeptide which is proteolitically processed to yield individual proteins. Because

of its molecular characteristics, GFkV was identified as the representative of a new genus denoted *Maculavirus*, of which it represents the type species, whilst GAMaV and GRVFV were assigned to the genus *Marafivirus*. Further physico-chemical, molecular and ultrastuctural studies disclosed sufficient similarities between maculaviruses, marafiviruses and members of the genus *Tymovirus* to warrant the establisment of the a new family denoted *Tymoviridae.* The current taxonomic classification of viruses of the fleck complex is therefore the following:

Order *Tymovirales*
Family *Tymoviridae*
Genus *Marafivirus*
Grapevine asteroid mosaic-associated virus
Grapevine rupestris vein feathering virus
Genus *Maculavirus*
Grapevine fleck virus
Grapevine redgloble virus

Cytopathology: GFkV infections are characterized by a severe modification of mitochondria into structures called "multivesiculate bodies", whereas GAMaV induces peripheral vesiculation of chloroplasts. These deranged organelles are thought to be sites of virus replication.

Transmission: No vector is known for any of the viruses of the fleck complex. Although observations from Italy, South Africa and Japan suggest natural field spread of GFkV and a similar behaviour was reported from Greece for a disease formerly thought to be asteroid mosaic but now identified as "grapevine rupestris vein feathering". Primary dissemination of these and the other viruses of the complex is through infected propagative material. Transmission through dodder of GFkV has been reported but it has no epidemiological relevance. GFkV is not seed transmitted.

Varietal susceptibility: GFkV and possibly all the other viruses of the complex infect naturally a large number of varieties and *Vitis* species. No information is available on individual susceptibility. Symptoms of asteroid mosaic have been observed in several cultivars grown in California: Merlot, Zinfandel (=Primitivo), Mission, Colombard, Carignane, Emperor, Thompson seedless and Valdepeñas.

Gographical distribution: Fleck has a worldwide distribution. The other members of the complex have been recorded so far from a limited number of countries.

Detection: Indexing on *V. rupestris* allows with a reasonable level of confidence the discrimination of the different viruses of the complex based on the differential reaction of the indicator. Polyclonal antisera and monoclonal antibodies to GFkV heve been raised. Therefore, ELISA is currently employed for routine detection of GFkV, but cannot be used for any of the other members of the complex due to the unvailability of antisera. Virus specific and degenerate primers have been designed for single or multiplex RT-PCR detection of GFkV, GRGV, GAMaV, and GRVFV.

Control: Because of the latency of symptoms sanitary selection of European grapevine cultivars and most American rootstock hybrids is ineffective. GFkV can be eliminated by heat therapy, meristem tip or fragmented shoot apex culture. The same sanitation procedures are likely to operate successfully with the other viruses of the complex, but no experimental data are available.

2. HISTORICAL REVIEW.

1954 **Hewitt**: First description of asteroid mosaic in California. As the disease is rare and does not appear to be spreading, its economic importance is low.

1962 **Hewitt** *et al.*: First record of fleck as an unidentified symptom different from fanleaf and transmissible from symptomless varieties to *V. rupestris* St. George.

1966 **Vuittenez** *et al.*: "Marbrure", a disease inducing symptoms similar to those of fleck in *V.rupestris* described in France.

1966 **Refatti:** Review paper on asteroid mosaic. Comparison of symptoms with those of other mosaic diseases of grape. Attempts to transmit the disease by mechanical inoculation to herbaceous test plants or by *Xiphinema index* were unsuccessful.

1970 **Refatti**: Symptoms resembling asteroid mosaic as described in California are reported from Italy and South Africa.

1972 **Bovey:** Identification of fleck in Switzerland as a latent disease of Chasselas transmissible to *V. rupestris.*

1972 **Hewitt** *et al.*: Description of fleck as an independent graft-transmissible disease present in many European varieties and American rootstocks.

1972 **Rives:** Further demonstration that fleck is distinct from fanleaf based on differential responses to heat treatment.

1973 **Ottenwaelter** *et al.*: Successful elimination of fleck through heat therapy.

1973 **Goheen and Luhn**: A novel heat therapy system based on virus inactivation in buds grafted onto healthy LN 33 rootstocks is effective against fleck.

1973 **Hévin** *et al.*: Fleck is not seed transmissible.

1974 **Milku**s: Suggestion of a prokaryotic etiology for fleck.

1977 **Mink and Parsons**: Use of a growth chamber with controlled temperature for a quicker and improved symptom expression of fleck and other virus or virus-like diseases (fanleaf, leafroll and corky bark).

1982 **Barlass** *et al.*: Successful elimination of fleck through fragmented shoot apex culture *in vitro.*

1983 **Verderevskaya** *et al.*: Observation of an isometric non mechanically transmissible virus in the phloem of diseased vines.

1983 **Castellano** *et al.*: Observation of a non mechanically transmissible virus, later called grapevine phloem-limited isometric virus (GPLIV), in sieve tubes of field-grown vines with leafroll symptoms but likely to be affected by other diseases. Report of multivesiculate inclusion bodies probably connected with GPLIV infection.

1983 **Woodham and Krake**: Dodder transmission of fleck from vine to vine.

1984 **Castellano and Martelli**: Confirmation that GPLIV is associated with multivesiculate bodies and demonstration that these derive from deranged mitochondria.

1985 **Castellano** *et al.*: Purification of GPLIV from naturally diseased vines and production of a specific antiserum.

1985 **Savino** *et al.*: Report of widespread occurrence of fleck in visually selected grapevine clones in southern Italy. The efficiency of heat treatment for disease elimination is unsatisfactory.

1987 **Triolo and Materazzi**: Fleck has a detrimental effect on the quality *V. rupestris* propagating wood. Rooting ability and graft take are adversely affected.

1989 **Yamakawa**: Field spread of fleck in Japan.

1990 **Boulila** *et al.*: Physicochemical characterization of GPLIV. Confirmation that the virus can be eliminated by heat therapy and is not related to leafroll.

1990 **Dolja** *et al.*: Identification of a dsRNA of about 7 Kb pairs in diseased vines.

1990 **Engelbrecht and Kasdorf**: Observation of natural field spread of fleck in South Africa. Report that a virus serologically similar to GPLIV is associated with the disease.

1991 **Triolo and Resta**: Tetracycline treatments are ineffective against fleck. Dismissal of the prokaryote etiology hypothesis.

1991 **Gugerli** *et al.*: Report of the close association with fleck symptoms in *V. rupestris* of an isometric virus latent in *V. vinifera.*

1991a **Boscia** *et al.*: Report of a highly consistent association of GPLIV with fleck in naturally infected and graft-inoculated *V. rupestris.* Meristem tip culture effectively eliminates the virus.

1991b **Boscia** *et al.*: GPLIV shown to be the agent of fleck. Virus renamed *Grapevine fleck virus* (GFkV). ELISA used successfully for virus detection in large scale surveys.

1991 **Kyriakopoulou**: Description of a disease similar to asteroid mosaic observed in *V. vinifera* cv. Sultanina in Greece. Symptoms are severe and affected vines are almost fruitless. The disease seems to be spreading naturally.

1991 **Namba** *et al.*: A spherical virus purified from berries of Ajinashica disease-affected vines is serologically related to GPLIV (=GFkV) and has physicochemical properties comparable to those of GFkV.

1993 **Walter and Cornuet**: Confirmation by ELISA of the consistent association of GFkV with fleck disease. June-July are the best months for ELISA detection of the virus in Alsace (France).

1993 **Kyriakpoulou** *et al*: Graft transmission of the putative asteroid mosaic syndrome found in Greece to *V. rupestris*. Symptoms consist of "vein clearing-yellowing". On this basis the disease was identified as asteroid mosaic.

1994 **Boscia** *et al.*: A non mechanically transmissible isometric virus similar but unrelated to GFkV identified in asteroid mosaic-infected grapevines. Virus named Grapevine asteroid mosaic-associated virus (GAMaV).

1995 **Boscia** *et al.*: Two GFkV-specific monoclonal antibodies raised in Italy can successfully be used in ELISA.

1995 **Kuniyuki and Costa**: Three strains of GFkV reported from Brasil, based on the differential reactions of indicatore.

1996 **Credi and Babini**: Infection by fleck, vein necrosis and vein mosaic has a detrimental effect on rootstock growth. Pruning wood is reduced by 51% in 420A and by 37% in Kober 5BB. Adverse effect on Teleki 5A is negligible.

1996 **Fortusini** *et al.*: Natural field spread of GFkV observed in Northern Italy.

1997 **Schieber** *et al.*: Additional monoclonal antibodies raised in France. One of these antibodies is more sensitive than the polyclonal antiserum for GFkV detection by ELISA.

1997 **Faoro and Gugerli**: An unidentified phloem-limited isometric virus serologically differing from GFkV observed in vines showing double-membraned peripheral invaginations of the chloroplast envelope. This cytological feature recalls that later found in vines infected by *Grapevine rupestris vein feathering virus.*

1998 **Marsumoto and Ohki**: A spherical virus resembling GFkV identified in thin sectioned cells of *V. rupestris* with a necrotic disease. GFkV-like multivesiculate bodies derived from deranged mitochondria are present in infected cells.

2000 **Sabanadzovic** *et al.*: Use of degenerate primers designed on the methyl transferase and polymerase cistrons of members of *Tymovirus* and *Marafivirus* genera and of GFkV amplified a genome fragment of GFkV, GAMaV and of another virus with GFkV-like particles phylogenetically but not serologically related to GFkV present in a cv Red globe vine. Virus named *Grapevine redglobe virus* (GRGV).

2001 **Sabanadzovic** *et al.*: Complete nucleotide sequence of the GFkV genome. Molecular properties of this virus further support the notion that it warrants classification in a genus of its own.

2001 **Elbeaino** *et al.*: Molecular reagents (degenerate primers) developed for the specific identification of viruses of the fleck complex (GFkV, GAMaV, GRGV). Detection of sequences of an undentified virus from a Greek grapevine, later named Grapevine rupestris vein feathering virus (GRVFV).

2002a **Martelli** *et al.*: Description of *Maculavirus*, a new genus of plant viruses having GFkV as type species and GRGV as tentative species.

2002b **Martelli** *et al.*: Description of the family *Tymoviridae*, comprising the genera *Maculavirus* and *Marafivirus* that include GFkV/GRGV and GAMaV/GRVFV, respectively.

2003a **Abou Ghanem-Sabanadzovic** *et al.*: Sequencing of the 3' end of the genome of GRGV, GAMaV and of a virus of Greek origin which induces vein feathering in *V. rupestris* confirms the assignment of GRGV to the genus *Maculavirus* and of GAMaV and the Greek virus to the genus *Marafivirus*. Greek virus recognized as a species in its own right denoted *Grapevine rupestris vein feathering virus* (GRVFV).

2003b **Abou Ghanem-Sabanadzovic** *et al.*: Development of a multiplex RT-PCR protocol for the simultaneous detection of GFkV-like viruses using plant mRNA as an internal control. GRVFV recorded from California and confirmation that GAMaV does not occur outside of California.

2003 **Shi** *et al.*: A sequence variant of GFkV (GFkV416) with a 63 nucleotide insertion in the replicase gene identified in Australia and New Zealand. In other countries (USA, South Africa, Argentina, Iran, and Japan) only the variant without insertion (GFkV353) was detected.

2004 **Fajardo** *et al.*: GFkV in Brazil.

2011 **Glasa** *et al.*: Identification of two distinct molecular groups of GFkV.

2011 **Dreher** *et al.*: Updated taxonomic position of viruses of the fleck complex.

2012 **Spring** *et al.*: The presence of GFkV worsens the performance of cv. Gamay vines infected by GLRaV-1.

2012 **Lekikot** *et al.*: GFkV in Algeria.

2012 **Komorowska** *et al.*: GFkV in Poland.

2012 **Mannini** *et al.:* Elimination of GFkV from apparently singly infected cv. Nebbiolo vines decreases the yield but improved the qualitative parameters.

2012 **Fiore** *et al.*: First record of Grapevine rupestris vein feathering virus (GRVFV) in Spain with an incidente of 7%.

2012 **Spilmont** *et al.*: Highly efficient elimination of GFkV (100%) by micrografting on cv. Vialla seedlings.

2012 **Faggioli** *et al.* Protocol for detection of grapevine viruses included in the Italian certification scheme (GFkV).

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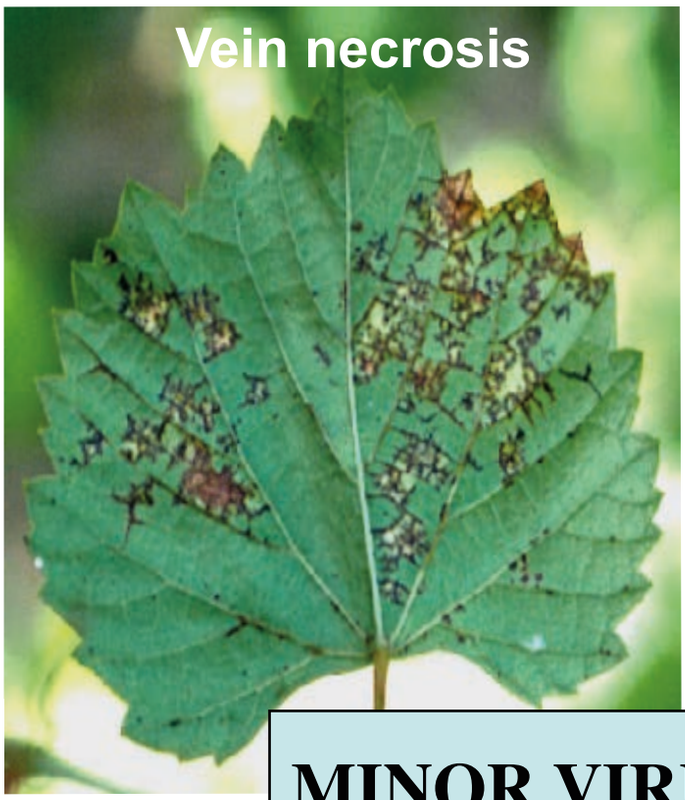
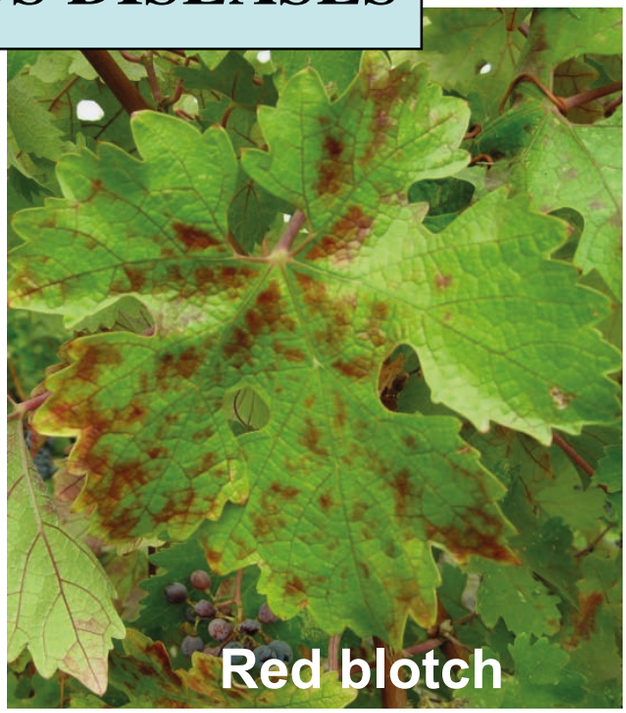


MINOR VIRUS DISEASES



MINOR VIRUSES AND VIRUS DISEASES

Several graft-transmissible diseases are known, with which specific viruses are associated and thought to be their possible causal agents. Some of these diseases have been recorded only from Europe, others occur in Japan and in the USA. Their overall importance is minor if compared with that of the major diseases dealt with in previous chapters, but some are of economic relevance locally, e.g. those induced by *Grapevine berry inner necrosis virus* (GBNV), Grapevine Pinot gris virus (GPGV), Grapevine vein clearing virus (GVCV) and Grapevine red blotch-associated virus. In addition several viruses have been found for which a cause/effect relationship with a specific malady has not been established. For practical purposes these viruses are assigned to the geographical area they were first recorded from. Interestingly, some these viruses have been discovered using a "deep sequencing" technology, either starting form the analysis of small interfering RNA populations (Kreuze *et al*., 2009; Wu *et al*., 2010) or from cDNA libraries of fragmented double-stranded RNAs of viral origin (Coetze *et al*., 2010). Deep sequencing has also diclosed that the "virome" of grapevine plants comprises a wide array of mycovirus sequences (Al Rwahnih *et al*., 2011) which may derive from fungal pathogens and endophytes.

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A. WORLDWIDE DISEASES

VEIN NECROSIS

Vein necrosis is a disease that shows on vines of the rootstock *V. rupestris* × *V. berlandieri* 110 Richter used as indicator in routine indexing assays. Since an association has been found between some strains of *Grapevine rupestris stem pitting-associated virus* (GRSPaV) and 110R vines with vein necrosis symptoms, the hypothesis was put forward that vein necrosis is a reaction of the rootstock 110R to infection by specific GRSPaV strains. Because of this, it should be kept in mind that vein necrosis could find a more appropriate allocation among the rugose wood syndromes.

1. DESCRIPTION

Main synonyms: Nécrose des nervures (Fr.), Adernnekrose (Germ.), necrosi delle nervature (Ital.).

Main symptoms: On the rootstock 110R, growth is much reduced and necrosis of the leaf veins appears, at first on the leaves at the base of the shoots, later on younger leaves as they develop. Necrotic reactions are best seen at the lower face of the leaf blade. Also the tendrils and shoots can necrotize, especially under greenhouse conditions, and some infected plants may die.

Agent: There is a clear-cut association between the disease and some GRSPaV strains. Phytoplasmas have been observed in the phloem of symptomatic vines, but current knowledge supports the notion that they do not have any aetiological relationship with the disease.

Transmission: By grafting and vegetative propagation. No vector known.

Varietal susceptibility and sensitivity: The rootstock 110R is most sensitive. Little is known about sensitivity of other *Vitis* species, varieties or hybrids. In general, grapevine cultivars and rootstocks other than 110R are symptomlessly infected. So far, the economic importance of the disease has not been determined. The only *Vitis* species which is clearly affected is the rootstock hybrid 110R (*V. berlandieri* × *V. rupestris*).

Geographical distribution: Very extensive, perhaps worldwide, linked with the presence of the VN-inducing strains of GRSPaV.

Detection: By grafting on 110R. RT-PCR with virus specific primers and Western blot with an antiserum to recombinant coat protein of GRSPaV allow sensitive and reliable detection of this virus in symptomatic 110R plants.

Control: Use of indexed planting material. The agent of vein necrosis can be eliminated by heat therapy.

2. HISTORICAL REVIEW.

1973 **Legin and Vuittenez**: Discovery and description of vein necrosis while searching for indicators for fleck.

1978 **Milkus and Kalashyan**: Mycoplasma-like organisms found in phloem tissues of vines with vein necrosis. Cause-effect relationships between MLOs and the disease has never been ascertained.

1978 **Martelli** *et al.:* Vein necrosis in Italy and Bulgaria.

1984 **Woodham and Krake**: Vein necrosis in Australia.

1985 **Savino** *et al.*: In southern Italy, the incidence of vein necrosis in visually selected stocks of table and wine grape varieties averages 71%. Heat therapy reduced this value to 36%, but did not eliminate the disease entirely.

1986 **Lehoczky** *et al.*: Vein necrosis in Hungary.

1988 **Gursoy**: Vein necrosis in Turkey.

1989 **Rumbos**: Vein necrosis in Greece.

1992 **Martelli** *et al.*: Vein necrosis in Malta.

1993 **Golino**: Vein necrosis in California.

1994 **Khun:** Vein necrosis in Brazil.

2005 **Bouyahia** *et al.*: An association exceeding 95% observed between GRSPaV and 110R vines showing vein necrosis symptoms in indexing trials. No vein necrosis observed in 110R top grafted on GRSPaV-free *V. rupestris*. Suggestion than vein necrosis is a specificic reaction of 110R to GRSPaV.

2011 **Morelli** *et al.:* GRSPaV-MG, a novel strain of GRSPaV, and GRSPaV-SG1 (group 2a) do not induce pitting in *V. rupestris* but both cause vein necrosis.

2012 **Alliaume** *et al.*: Presence of GRSPaV group 2 isolates does not necessarily induce vein necrosis

2012 **Della Bartola** *et al.:* Not all isolates of group 2a (SG1 lineage) and 2b (RSPaV-1 lineage) of GRSPaV induce vein necrosis.

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B. European diseases

GRAPEVINE YELLOW MOTTLE
(*Alfalfa mosaic virus*)

1. DESCRIPTION.

Main synonyms: None.

Main symptoms: Various patterns of yellow discolouration characterize the disease. The spring growth shows more or less extensive yellowing of the leaf blades that does not extend to the veins. Faint yellow speckling, rings and lines are typical summer responses of infected vines. Plant vigour and yield do not seem appreciably affected.

Agent: *Alfalfa mosaic virus* (AMV), the type species of the genus *Alfamovirus*, is the putative causal agent of the disease. AMV, a mechanically transmissible virus, has differently shaped particles, from quasi isometric to bacilliform, 30 to 57 nm in size, and a tripartite RNA genome accounting for *ca.* 18% of the particle weight, with the following mol. wts: RNA-1, 1.04×10^6 Da (3,644 nt); RNA-2, 0.73×10^6 Da (2,593 nt); RNA-3, 0.62×10^6 Da (2,037 nt). Capsid proteins subunits are of one type, with M_r 24×10^3 Da.

Transmission: AMV is efficiently transmitted by aphids in a non persistent manner and can cause epidemic outbreaks in many of its natural hosts. In grapevines, however, infections are scattered and occasional, suggesting that the virus spreads primarily through infected planting material.

Varietal susceptibility: Little information available. There may be differential susceptibility among cultivars.

Geographical distribution: Yellow mottle has been reported from Germany, Switzerland, Hungary, former Czechoslovakia, Bulgaria, and Turkey.

Detection: AMV is mechanically transmissible to herbaceous hosts and can also be identified by ELISA and moleculat techniques in infected vines.

Control: Use of healthy material obtained by heat treatment.

2. HISTORICAL REVIEW.

1973 **Bercks** *et al.*: First record of AMV infections and description of symptoms in German grapevines.

1975 **Bovey and Brugger**: AMV recorded from Switzerland in grapevine and transmitted by grafting to *V. rupestris* and the hybrid Grézot 1×5C.

1976 **Novak and Lanzova**: AMV infections recorded from hop and grapevine in Czechoslovakia.

1979 **Bovey and Cazelles**: AMV particles visualized in thin sectioned grapevine leaves. Virus elimination by treating for 37 days at 37-38°C.

1978 **Jankulova**: AMV in Bulgaria.

1981 **Beczner and Lehoczky**: AMV in Hungary. Chardonnay and Veltliner rouge précoce identified as reliable indicators.

1985 **Francki:** Comprehensive review of the properties of AMV an other viruses with tripartite genome

1993 **Martelli**: Yellow mottle suggested as the name for the disease caused by AMV in grapevines.

1993 **Akbas and Erdiller:** AMV in Turkey.

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GRAPEVINE LINE PATTERN

1. DESCRIPTION.

Main synonyms: None.

Main symptoms: Leaves show bright yellow discolourations that form marginal rings, scattered spots or blotches, or maple leaf-like line patterns typically confined to the petiolar area, or the upper part of the blade, roughly following its contour. Vigour and yield are reduced.

Agent: The putative agent, Grapevine line pattern virus (GLPV) a possible member of the genus *Ilarvirus*, has differently shaped particles, quasi spherical 25-30 nm in diameter to bacilliform 40 to 75 nm in length, and a multipartite genome.

Transmission: GLPV has no known vector, is seed-transmitted and spreads with diseased propagative materials.

Varietal susceptibility: No information. Several *V. vinifera* cultivars are susceptible.

Geographical distribution: Reported only from Hungary.

Detection: GLPV is mechanically transmissible to herbaceous hosts. Graft transmission to cv. Jubileum 75.

Control: No information.

2. HISTORICAL REWIEV.

1985 **Francki:** Comprehensive review of the properties of AMV an other viruses with tripartite genome.

1987 **Lehoczky** *et al.*: Description of line pattern disease in Hungary. Evidence that a graft- and mechanically transmissible virus is associated with it.

1989 **Lehoczky** *et al.*: Purification and characterization of GLPV and suggestion that it is the causal agent of the disease.

1992 **Lehoczky** *et al.*: Evidence that GLPV is transmitted through grapevine seeds.

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GRAPEVINE ANGULAR MOSAIC

1. DESCRIPTION

Main synonyms: None

Main symptoms: Symptoms are chlorotic angular spots on the leaf blades, discoloration of tissues bordering the veins, crinkling and deformation of the leaves. Infected grapevines are stunted, decline gradually and some die. Flowers abortion results in straggly bunches with small wrinkled berries bearing non viable seeds.

Agent: Grapevine angular mosaic virus (GAMV), a virus with a tripartite RNA genome and a 30 kDa coat protein, reproduced the field syndrome in mechanically inoculated grapevine seedlings, thus is regarded as the agent of the disease. GAMV is molecularly related to a number of ilarviruses, the closest being a group of species comprising *Tobacco streak virus* (TSV), *Parietaria mottle virus* (PMoV), Strawberry necrotic shock virus (SNSV) and Blackberry chlorotic ringspot virus (BCRS), but differs from Grapevine leaf pattern virus, the only other ilarvirus reported from grapevine.

Transmission: GAMV is pollen-borne in herbaceous hosts and was able to infect pollinated plants. However the virus is not seed-transmitted in the grapevine. There was no transmission by aphids. Infected grafting material is likely to be responsible for virus dissemination.

Varietal susceptibility: No information.

Geographical distribution: Reported only from Greece.

Detection: Indexing on cv. Baresana x Baresana, mechanical transmission to herbaceous hosts, and ELISA.

Control: *In vitro* heat therapy combined with meristem tip culture is very effective in virus elimination.

2. HISTORICAL REVIEW

2000 **Girgis** *et al.*: First record of GAMV.

2003 **Girgis** *et al.*: Evidence that GAMV is the agent of grapevine angular mosaic disease.

2006 **Grammatikaki** *et al.*: GAMV is readily eliminated by *in vitro* heat therapy and meristem tip culture.

2009 **Girgis** *et al.*: Thorough characterization of GAMV.

3. REFERENCES

Girgis S.M., Bem F. P., Kyriakopoulou P.E., Dovas C.I., Sklavounos A.P., Avgelis A., Katis N., Tzortzakakis S., Tsagris M., 2000. A new ilarvirus isolated from grapevine in Greece. *Plant Disease* **84**: 1345

Girgis S.M., Bem F.P., Kyriakopoulou P.E., Dovas C.I., Avgelis A., Katis N., 2003. The etiology of a new virus disease: grapevine angular mosaic. *Extended Abstracts 14th Meeting of ICVG, Locorotondo, Italy*: 19.

Girgis S.M., Bem F.P., Dovas C.I., Sclavounos A., Avgelis A.D., Tsagrig M., Katis N., Kyriakopoulou P.E., 2009. Characterization of a novel ilarvirus causing grapevine angular mosaic disease. *European Journal of Plant Pathology* **125**: 203-211.

Grammatikaki G., Girgis S.M., Avgelis A., 2006. Elimination of Grapevine angular mosaic virus (GAMV) by heat reatment and meristem shoot tip culture. *Extended Abstract 15th Meeting of ICVG, Stellenbosch, South Africa*: 153-154.

GRAPEVINE YELLOW LINE PATTERN
(Rasperry bushy dwarf virus)

1. DESCRIPTION

Main synonyms: None

Main symptoms: Infected vines of cv. Laski Rizling from Slovenia exhibit a yellow line pattern syndrome resembling the grapevine line pattern disease described from Hungary.

Agent: *Raspberry bushy dwarf virus* (RBDV) was isolated from symptomatic vines. RBDV, the type species of the genus *Idaeovirus*, is a pollen- and seed-borne virus with quasi spherical particles made up of a sigle type of coat protein subunits (M_r *ca.* 30×10^3), a diameter of about 33 nm, and a bipartite single-stranded RNA genome accounting for *ca.* 24% of the particle weight and consisting of two functional species: RNA-1 with mol. wt of 2×10^6 Da (5.5 Kb in size) and RNA-2 with mol. wt 0.8×10^6 Da (2.2 Kb in size). In phylogenetic trees constructed with the coat protein sequences, grapevine viral isolates group in a clade different from those comprising isolates from red and black raspberries and *Rubus multibracteatus*. The virus is irregularly distributed in field-infected vines.

Transmission: In raspberry, the virus infects progeny seedlings (up to 77%) and pollinated plants through pollen. Seed transmission in grapevine does not occur. The vay of natural spreading in grapevine is suspected to be mediated by nematodes since the virus was detected by nested RT-PCR in a few individuals of *Longidorus juvenilis*. Infected propagative material is responsible for medium and long distance virus disseminatation.

Varietal susceptibility: Virus detected in several cultivars of white- and red-berried grapevine wine varietes.

Geographical distribution: Reported from several viticultural areas of Slovenia., Hungary and Serbia.

Detection: Mechanical transmission to herbaceous hosts, ELISA, and RT-PCR. Monoclonal antibodies can differentiate grapevine from raspberry isolates.

Control : No information

2. HISTORICAL REVIEW

1976 **Murant**: Description of RBDV.

2003 **Mavric** *et al.*: First record of RBDV in grapevine.

2006 **Mavric and Virscek Marn**: Virus is iregularly distributed in infected vines.

2006 **Virscek Marn and Mavric**: Virus detection in different Slovenian grapevine cultivars.

2009 **Mavric Plesko** *et al.*: Biological, serological and molecular characterization of the grapevine strain of RBDV.

2011 **Jevremovic and Paunovic**: Virus reported from Serbia.

2012 **Mavric Plesko** and **Virscek Marn**: Virus reported from Hungary.

3. REFERENCES

Jevremovic D., Paunovic S., 2011. Raspberry bushy dwarf virus – a grapevine pathogen in Serbia. *Pesticide and Phytomedicine (Belgrade)* **26**: 55-60.

Mavric I., Virscek Marn M., Zezlina I., 2003. Raspberry bushy dwarf virus infection of grapevine in Slovenia. *Extended Abstracts 14th Meeting of IGVG, Locorotondo, Italy*: 20.

Mavric I., Virscek Marn M., 2006. Preliminary results show irregular distribution of Raspberry bushy dwarf virus in

infected grapevines. *Extended Abstracts 15th Meeting of ICVG, Stellenbosch, Sout Africa*: 234.

Mavric Plesko I., Virscek Marn M., Sirca S., Urek G., 2009. Biological, serological and molecular characterization of *Raspberry bushy dwarf virus* from grapevine and its detection in the nematode *Longidorus juvenilis*. *European Journal of Plant Pathology* **123**: 261-268.

Mavric Plesko I., Virscek Marn M., 2012. First report of *Raspberry bushy dwarf virus* infecting grapevine in Hungary. *Plant Disease* **96**: 1582-1583.

Murant A. F., 1976. Raspberry bushy dwarf virus. *CMI/AAB Description of Plant Viruses,* No. 165

Virscek Marn M., Mavric I., 2006. The occurence of *Raspberry bushy dward virus* in different grapevine varietes in Slovenia. *Extended Abstracts 15th Meeting of ICVG, Stellenbosch, South Africa*: 266-267.

GRAPEVINE LEAF MOTTLING AND DEFORMATION (*Grapevine Pinot gris virus*)

1. DESCRIPTION

Main synonyms: None

Main symptoms: Symptoms resemble those induced by nepoviruses, i.e. chlorotic mottling, puckering and deformation of the leaves, stunting, reduction of the quantity and quality of the yield. Infected vines of cv. Tamnara, a *V. vinifera* × *V. labrusca* hybrid grown in South Korea show poor fruit set and berries with internal necrosis.

Agent: A virus with filamentous particles denoted *Grapevine Pinot gris virus* (GPGV) is consistently associated with diseased vines. The viral genome is a single-stranded positive-sense RNA which has been assembled from libraries of the siRNAs population extracted from vines and deep sequenced by Illumina technology. The complete sequence of the genomic RNA encompasses 8,725 nucleotides, organized in three open reading frames (ORFs) which in the 5' → 3' direction encode: (i) a polypetide 214 kDa in size comprising the replication-associatated proteins (methyltransferse, helicase and RNA-dependent RNA polymerase) (ORF1); (ii) the 46 kDa movement protein (ORF2) and (iii) the 22 kDa coat protein. The 5' and 3' untranslated regions are 94 and 82 nt long, respectively. The 3' end is polyadenylated. The structural organization of the viral genome is identical to that of members of the genus *Trichovirus* with which GPGV is phylogenetically related. In phylotrees the virus groups in the same clade with *Grapevine berry inner necrosis virus* (GINV) with which it shows an identity at the amino acid level of 66% (ORF1), 65% (ORF2) and 71% (ORF3). The two viruses, however, are retained as different species. The coat protein of the South Korean strain of the virus is 97% identical to the comparable gene of GPGV.

Transmission: Virus is graft-transmissible and seems to be spreading naturally, as shown by an increase from 15 to 34% of infected Pinot noir vines in the vineyards of Trentino and Friuli Venezia Giulia (north-eastern Italy) in a 3-year period (2010-2012). However, the way of spreading has not yet been ascertained. Although the virus was found by RT-PCR in pools of individuals of the grape erineum or blister mite *Colomerus vitis* collected from diseased vines, the results of transmission trials to grapevine seedlings were inconclusive. It should be noted that *C. vitis* is the alleged vector of the related GINV.

Varietal susceptibility: cv. Traminer is more strongly affected than cvs Pinot gris, Pinot noir and Glera.

Geographical distribution: Reported from northern Italian regions (Emilia-Romagna, Veneto, Trentino, Friuli Venezia Giulia), Slovakia, Slovenia, Czeck Republic, Greece and Korea.

Detection: RT-PCR using virus-specific primers.

Control: No information

2. HISTORICAL REVIEW

2012 **Giampetruzzi** *et al.*: Identification and molecular characterization of *Grapevine pinot gris virus.*

2013 **Cho** *et al.*: GPGV reported from South Korea.

2013 **Berber** *et al.*: Transmission trials of GPGV with the grape blister mite *Colomerus vitis* have given inconclusive results.

2013 **Beber** *et al.*: GPGV found in northern Italian regions (Emilia-Romagna and Veneto).

2013 **Saldarelli** *et al.*: Update on the disease induced by GPGV.

2014 **Mavric Plesko** *et al.*: GPGV in Slovenia.

2014 **Maliogka and Katis** : GPGV in Greece.

2014 **Glasa** *et al.*: GPGV in Slovakia and Czech Republic**.** Slovak virus isolates diverge from the Italian strain by up to 4.5%. Possible recombination bteween Slovak isolatea and *Grapevine berry inner necrosis virus* dtected in the 5' extremity of the viral genome.

3. REFERENCES

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F., 2013. Transmission trials of *Grapevine Pinot gris virus* by the eriophyoid mite *Colomerus vitis*. *Journal of Plant Pathology* **95**: S4.36.

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Cho I.S., Jung S.M., Cho J.D., Choi G.S., Lim H.S., 2013. First report of Grapevine Pinot gris virus infecting grapevine in Korea. *New Disease Reports* **27**: 10.

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Raiola A. Scopel C., Ferrigno D., Taglietti F., Duso C., Causin R., 2013. First report of Grapevine Pinot gris virus infecting cv. Glera in the Conegliano-Valdobbiadene D.O.C.G. *Journal of Plant Pathology* **95**: S4.58.

Saldarelli P., Beber R., Novelli L., Bianchedi P., Credi R., Giampetruzzi A., Malossini U., Pirolo P., Poggi Pollini C., Ratti C., Terlizzi F., Gualandri V., 2013. Studies on a new grapevine disease in Trentino vineyards. *Journal of Plant Pathology* **95**: S4.60.

C. Japanese diseases

GRAPEVINE BERRY INNER NECROSIS

1. DESCRIPTION

Main synonyms: None

Main symptoms: Infected grapevines have low vigour, delayed bud break and shoots with short internodes and internal browning. Leaves show chlorotic mottling, rings and line patterns. Ripening of bunches is delayed, berries are small and show external discolorations and internal necrosis. The disease has been reported only from Japan, representing the most important virus disorder in Yamanashi Prefecture.

Agent: Disease agent is *Grapevine berry inner necrosis virus* (GINV), a mechanically transmissible definitive member of the genus *Trichovirus*. GINV has filamentous particles about 750 nm in length and a single-stranded RNA genome with mol. wt of 7.5x106 Da, the 3' terminal region of which (2,469 nts) has been sequenced.

Transmission: GINV is transmitted by grafting to grapevines and by mechanical inoculation to herbaceous hosts. The virus spreads naturally in the vineyards, being transmitted by the eryophid mite *Colomerus vitis.* Healthy vines of cvs Kyoho and Pione became naturally infected in the field within one year from planting.

Varietal susceptibility: Symptom severity varies with the cultivar. Almost all Japanese table grape cultivars derived from crosses with cv. Campbell Early are suscetible as well as cvs Takao, Kyoho, and Pione, whereas cvs. Delaware, Koshu and Kaiji are infected latently. Some rootstocks (e.g. *Vitis riparia* Gloire) are also susceptible.

Geographical distribution: Reported only from Japan.

Detection: Indexing on cvs Kyoho or Pione. GINV is mechanically transmissible to herbaceous hosts and can be identified by ELISA and moleculat techniques in infected vines.

Control: Use of tolerant cultivars in areas where the disease spreads epidemically.

2. HISTORICAL REVIEW

1984 **Tanaka**: Description of a mosaic disease in cv. Kyoho in Japan.

1985 **Yanase**: Purification of a filamentous virus isolated from mosaic-diseased grapevines.

1987 **Yanase and Terai**: Induction of mosaic symptoms in grapevines inoculated with the filamentous virus.

1992 **Terai and Yanase**: Induction of berry internal necrosis in cv. Kyoho back inoculated with the filamentous virus isolated from mosaic-diseased grapevines. Disease re-named Grapevine berry inner necrosis.

1993 **Terai** *et al.*: First account of grapevine berry inner necrosis disease in a non Japanese publication.

1997 **Yoshikawa** *et al.*: Partial sequencing of GINV genome and assignement of the virus in the genus *Trichovirus.*

2000 **Nishijima** *et al.*: An account of the varietal susceptibility to the disease and natural field spread.

2000 **Kunigi** *et al.*: Experimental evidence that GINV is transmitted by the the grape erineum mite *Colomerus vitis.*

2006 **Yoshikawa** *et al.*: Transgenic *Nicotiana occidentalis* plants expressing a movement protein (P50) and

partially functional deletion mutants (DeltaA and DeltaC) of *Apple chlorotic leaf spot virus* (ACLSV) show resistance to GINV due to the interference of both long-distance and cell-to-cell movement of the virus.

3. REFERENCES

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Nishijima T., Terai Y., Kunugi Y., 2000. Studies on the grapevine berry innner necrosis virus disease. 1. Symptoms on vines, varietal susceptibility and natural spread. *Bulletin of Yamanashi Fruit Tree Experimental Station* **10**: 47-56.

Tanaka H., 1984. Mosaic symptoms on cv Kyoho. *Annals of the Phytopathological Society of Japan* **55**: 536-538

Terai Y., Yanase H., 1992. Induction of berry necrosis in Kyoho back-inoculated with the virus isolate from grapevine mosaic diseased clones and renaming to grapevine berry inner necrosis. *Annals of the Phytopathological Society of Japan* **58**: 617-618

Terai Y., Kunigi Y., Yanase H., 1993. A new virus disease, grapevine berry inner necrosis with natural spread in Japan. *Extended Abstracts 11th Meeting of ICVG, Montreux, Switzerland*: 77-78

Yanase H., 1985. Purification of a filamentous virus isolated from grapevine berry inner necrosis and foliar mosaic. *Annals of the Phytopathological Society of Japan* **51**: 362-365.

Yanase H., Terai Y., 1987. Back-transmission of a grapevine filamentous virus to grapevine seedlings and induction of foliar and berry symptoms in grapevine. *Annals of the Phytopathological Society of Japan* **53**: 423.

Yoshikawa N., Iida H., Goto S., Magome H., Takahashi T., Terai Y., 1997. Grapevine berry inner necrosis, a new trichovirus: comparative studies with several known trichoviruses. *Archives of Virology* **142**: 1351-1363

Yoshikawa N., Saitou Y., Kitajima A., Chida T., Sasaki N., Isogai M., 2006. Interference of long-distance movement of Grapevine berry inner necrosis virus in transgenic plants expressing a defective movement protein of Apple chlorotic leaf spot virus. *Phytopathology* **96**: 378-385.

GRAPEVINE STUNT

1. DESCRIPTION.

Main synonyms: None.

Main symptoms: Spring vegetation is delayed, internodes are short, leaves are small, curled and, sometimes, with scorched margins. Inflorescences are undersized, fruit setting is impaired and bunches are few and shelled. Because of heat recovery, summer vegetation is apparently normal.

Agent: An isometric, phloem-limited, non mechanically transmissible virus about 25 nm in diameter is consistently associated with diseased vines and regarded as the possible causal agent. This virus is serologically distinct from the putative agent of ajinashika disease.

Transmission: The disease is transmitted by the leafhopper *Arboridia apicalis*. Spread occurs also through infected propagative material.

Varietal susceptibility: No information. The disease is apparently restricted to the *V. vinifera* cv. Campbell Early.

Geographical distribution: Reported only from Japan.

Detection: Grafting to cv. Campbell Early and ELISA using extracts from infected vine tissues.

Control: Use of disease-free material obtained through heat therapy.

2. HISTORICAL REVIEW.

1981 **Namba** *et al.*: A small isometric virus associated with stunt disease in Japan.

1982 **Hatamoto** *et al.*: Successful graft-transmission of stunt disease.

1984 **Hatamoto** *et al.*: Evidence that the disease is transmitted by the leafhopper *Arboridia apicalis*.

1986 **Namba** *et al.*: Purification and characterization of the virus associated with stunt disease. Evidence that it is not related to the presumed agent of ajinashika disease.

3. REFERENCES

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Namba S., Yamashita S., Doi Y., Yora K., 1981. A small spherical virus associated with grapevine stunt disease. *Annals of the Phytopathological Society of Japan* **47**: 137.

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Crops in the Tropics and Subtropics, p.109-126. FFTC Book series, No. 33. Food and Fertilizer Technology Center for the Asian and Pacific Region, Taipei, Taiwan (Reference 2951 in the *Review of Plant Pathology* **66**: 316, 1987). The same paper appears in *Taiwan Food and Fertilizer Technology Center Technical Bulletin* **92**: 1-17.

GRAPEVINE AJINASHIKA DISEASE

1. DESCRIPTION.

Main synonyms: none.

Main symptoms: No appreciable symptoms are visible on the foliage of cv. Koshu nor any apparent reduction of vigour and yield. The berries, however, are pale-coloured and have a low sugar content, which makes the crop unmarketable. This condition gives the name to the disease which in Japanese means "unpalatable fruits with low sugar content". American rootstocks are infected without showing symptoms.

Agent: The disease was reported to be caused by the concurrent infection of leafroll and fleck. However, an isometric, phloem-limited, non mechanically transmissible virus about 25 nm in diameter, consistently found in infected vines, was suggested as the possible causal agent.

Transmission: No vector is known. Dissemination is through infected propagative material.

Varietal susceptibility: No information. The disease seems to be restricted to *V. vinifera* cv. Koshu.

Geographical distribution: Reported only from Japan.

Detection: Graft transmission to cv. Koshu and ELISA using extracts from infected vine tissues.

Control: Use of disease-free material obtained through heat therapy.

2. HISTORICAL REVIEW.

1979 **Namba** *et al.*: First mention of ajinashika disease and report of the association with it of a non mechanically transmissible virus with isometric particles.

1980 **Terai and Yano**: Description of ajinashika disease and suggestion that it is caused by the concomitant infection of leafroll and fleck.

1986 **Namba** *et al.*: Partial characterization of the isometric virus associated with the disease and its detection by ELISA in infected vines. No relationship found with fleck.

1991 **Terai**: Additional report on ajinashika disease as derived from the combined effect of leafroll and fleck.

1991 **Namba** *et al.*: Further characterization of the isometric virus and claim that it is the putative agent of the disease.

3. REFERENCES

Namba S., Yamashita S., Doi Y., Yora K., 1979. A small spherical virus associated with the ajinashika disease of Koshu grapevine. *Annals of the Phytopathological Society of Japan* **45**: 70-73.

Namba S., Iwanami T., Yamashita S., Doi Y., Hatamoto M., 1986. Three phloem- limited viruses of grapevine: direct fluorescence detection. *Taiwan Food and Fertilizer Technology Center Technical Bulletin* **92**: 1-17.

Namba S., Boscia D., Yamashita S., Tsuchizaki T., Gonsalves D., 1991. Purification and properties of spherical virus particles associated with grapevine ajinashika disease. *Plant Disease* **75**: 1249-1253.

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D. NORTH AMERICAN DISEASES PUTATIVELY CAUSED BY DNA VIRUSES

Up to 2011 no virus with a DNA genome was found in grapevines. However, since 2009 it was known that the genome of a clone of cv. Pinot noir incorporated fragments of DNA sequences of pararetroviruses: i.e. six fragments of *Carnation etched ring virus* (CERV, genus *Caulimovirus*), five fragments of *Rice tungro bacilliform virus* (RTBV, genus *Tungrovirus*), two fragments each of *Strawberry vein banding virus* (SVBV, genus *Caulimovirus*) and *Lamium leaf distortion virus* (LLDV, genus *Caulimovirus*), and one fragment of *Cauliflower mosaic virus* (CaMV, genus *Caulimovirus*) (Bertsch *et al.*, 2009). These viral genome bits were suggested to act as "natural transgenes" that protected the vine from infection by the parent viruses, as their presence induced a form of resistance through a post-transcriptional gene silencing mechanism. Whether this is so remains to be experimentally proven. The point remains, however, that over time (some?) grapevines have

come in contact with DNA viruses, parts of whose genome found the way to integrate in the host genome.

Bertsch C., Beuve M., Dolja V.V., Wirth M., Pelsy F., Herrbach E., Lemaire O., 2009. Retention of the virus-derived sequences in the nuclear genome of grapevine as a potential pathway to virus resistance. *Biology Direct* **4**: 21.

GRAPEVINE VEIN CLEARING

1. DESCRIPTION

Main synonyms: None

Main symptoms: In early spring, infected vines show a narrow strip of chlorotic tissues along the major and minor veins of fully expanded leaves of young shoots. Chlorotic veins are translucent when the symptomatic leaves are held against sunlight, this representing a characterizing symptom with diagnostic significance. Young shoots have short internodes with zigzag growth. Mature leaves are small-sized, deformed and display various patterns of chlorotic to yellowish tissues and rolled margins. In advanced stages of infection the vines become dwarfed, bear fewer bunches and may show decline symptoms.

Agent: The disease agent is thought to be Grapevine vein clearing virus (GVCV), a non mechanically transmissible virus with a double-stranded DNA genome (the first DNA virus ever found in *Vitis*) belonging in the genus *Badnavirus*. As such, GVCV is likely to have non enveloped bacilliform particles *ca.* 30×150 nm in size. The completely sequenced genome is a double-stranded circular DNA 7,753 bp in size, consisting of three open reading frames (ORFs) identifed on the plus strand, which code for two unknown proteins of 24 kDa (ORF1) and 14 kDa (ORF2), respectively, and of a polypeptide 220 kDa in size (ORF3) comprising movement protein, coat protein, reverse transcriptase and RNase H. GCVC is related to *Commelina yellow mottle virus* (ComYMV), a defintive specie of the genus *Badnavirus*, family *Caulimoviridae*, with which it groups in phylogenetic trees. The virus occurs as genetically diverse populations. A search for GVCV sequence fragments incorporated in the reference grapevine genome PN40024 yielded negative results.

Transmission: Virus is transmitted by grafting from grape to grape. The way of natural spreading in the vineyards is unknown. However, it should be noted that some badnaviruses are transmitted by pseudococcid mealybugs.

Varietal susceptibility: Information is scanty. However field infection has been found in *V. vinifera* cultivars and French hybrids

Geographical distribution: Reported from grapevine-growing states of the USA mid-west.

Detection: RT-PCR using virus-specific primers.

Control: No information.

2. HISTORICAL REVIEW

2007 **Qiu** *et al.:* First report a severe grapevine disease from Missouri suspected to be of viral origin.

2009 **Lunden** *et al.*: Characterization of the infectious origin of the grapevine vein clearing complex.

2011 **Zhang** *et al.*: Characterization and complete sequencing of the dsDNA genome of GVCV.

2012 **Guo** *et al*: GVCV clusters in molecularly divergent subgroups: three based on reverse transcriptase sequence, two based on zingc finger sequence.

REFERENCES

Guo Q., Zhang Y., Qiu W.P., 2012. Grapevine vein clearing virus exists as genetically diverse populations in seven grape varieties in three midwestern states. *Proceedings 17th Congress of ICVG, Davis, USA*: 106-107.

Lunden S., Meng B., Avery J.D., Qiu W.P., 2009. Characterization of grapevine vein clearing complex on Chardonnay. *European Journal of Plant Pathology* **126**: 135-144.

Qiu W.P., Avery J.D., Lunden S., 2007. Charaterization of a severe virus-like disease in Chardonnay grapevines in Missouri. *Plant Health Progress.* Doi 10.1094/PHP-2007-1119-01-BR.

Zhang Y., Singh K., Kaur R., Qiu W., 2011. Association with a novel DNA virus with the grapevine vein-clearing and vine decline syndrome. *Phytopathology* **101**:1081-1090.

GRAPEVINE RED BLOTCH

1. DESCRIPTION

Main synonyms: None

Main symptoms: Infected vines display patches of red blotches along the margins and red veins on the underside of the blade. The sugar content of the fruit juice is reduced. It is not known whether there are any effects on fruit yield or plant longevity.

Agent: A virus with circular single-stranded DNA genome with a structure comparable to that of members of the family *Geminiviridae* has been found in three USA states (NY, CA and WA). The NY isolate was provisionally called Grapevine Cabernet franc-associated virus (GCFaV) and the WA isolate Grapevine read leaf-associated virus (GRLaV). Since a "red leaf" symptomatology of grapevines is typically associated with disorders at the graft union (e.g. graft incompatibility) whatever their origin is, a discriminating name would be Grapevine red blotch-associated virus (GRBaV) or, more simply, Grapevine red blotch virus (GRBV) should a cause/effect relationship be established with the red blotch disease. The viral genome is 3,206 nt in size and contains six ORFs, three in the viral sense orientation and three in the complementary sense orientation. In phylogenetic trees, constructed with the CP, polymerase, or the full-length sequence, GCFaV forms a distinct branch, separate from those comprising members of the seven extant genera of the family *Geminiviridae*. This is the second geminivirus-like virus infecting a woody species, and the first ever found in grapevines.

Transmission: Transmitted by grafting and to healthy seedlings of different grape cultivars by *Erythroneura ziczac* (Viginia creeping leafhopper).

Varietal susceptibility: Symptoms observed on several red-berried cultivars.

Geographical distribution: Reported from the USA (New York, California and Washington) and British Columbia (Canada).

Detection: PCR with specifc primers using as template DNA extracted from leaf petioles or bark scrapings from dormant canes.

Control: No specific information is apparently available. However, disease management based on the production and use of sanitized propagating material would be desirable.

2. HISTORICAL REVIEW

2012 **Krenz** *et al.*: Description of a virus with a single-stranded cicular DNA genome (geminivirus-like) denoted Grapevine Cabernet franc-associated virus.

2013 **Al Rawhanih** *et al.*: Identification in Californian vines with red blotch symptoms of a virus seemingly identical to the putative geminivirus from NY state.

2013 **Poojari** *et al.*: A DNA virus denoted Grapevine readleaf virus found in vine with reddening symptoms in Wasington state (USA).

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E. North American RNA viruses of *Vitis vinifera*

GRAPEVINE SYRAH VIRUS 1

1. DESCRIPTION

Main synonyms: Grapevine virus Q (GVQ)

Main symptoms: The virus is symptomless in *Muscadinia* and may induce symptomless infections also in *V. vinifera*

Agent: GSyV-1 is a member of the genus *Marafivirus*, family *Tymoviridae* and has a single- stranded, bicistronic, positive-sense RNA genome 6,481 nucleotides in size. ORF1 codes for the replication-associated proteins (methytransferase, protease/endo/pepsidase, helicase, polymerase) and for the coat protein at the 3' terminus. ORF2 codes for the putative movement protein 27 kDa in size.

Transmission: Presumably the virus can be transmitted by grafting from vine to vine. It has been found in leafhoppers from plants showing Syrah decline but no correlation could be drawn between virus distribution and decline symptoms. The occurrence in hosts other than European grapes may be indicative of the action of a vector.

Varietal susceptibility: No information.

Natural host range: The virus has been recovered from *Vitis vinifera*, *Vitis aestivalis*, *Muscadinia rotundifolia* and *Rubus* spp.

Geographical distribution: This virus, originally reported from the USA, has now been descovered in Chile, Italy and Greece. Thus it may have a much wider distribution.

Detection: RT-PCR with virus specific primers.

Control: No information

2. HISTORICAL REVIEW

2009 **Al Rawhanih** *et al.*: Identification in a cv. Syrah vine affected by Syrah decline from California of Grapevine Syrah virus 1 (GSyV-1) and its characterization.

2009 **Sabanadzovic** *et al.*: Identification in an apparently healthy muscadine vine from Mississippi and characterization of a virus denoted Grapevine virus Q (GVQ). This virus is the same as GSyV-1.

2010 **Engel** *et al.*: GSyV-1 in Chile.

2011 **Giampetruzzi** *et al.*: GSyV-1 in Italy.

2014 **Maliogka and Katis**: GSyV-1 in Greece.

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Maliogka V., Katis N., 2014. Personal communication.

Sabanadzovic S., Abou Ghanem-Sabanadzovic N., Gorbalenya A.E., 2009. Grapevine virus Q: the first plant virus with a permuted active site of RNA-dependent RNA polymerase. *Virology* **394**: 1-7.

F. Viruses found in native North American *Vitis* species

This section contains the available information gathered during a survey carried out by S. Sabanadzovic and co-workers (Sabanadzovic S., 2009. Viruses of native *Vitis* germplasm in the southestern United States. *Extended Abstracts 16th Meeting of ICVG, Dijon, France*: 32-35) for the identification of viruses occurring in native *Vitis* species from the southeastern USA, either growing in culture (muscadines) or in wild environments (forests). Only two of these viruses, Grapevine cryptic virus 1 (GCV-1) and Summer grape latent virus (SGLV) have been characterized molecularly and are briefly decribed hereafter. All the remaining viruses are just listed in Table 1.

GRAPEVINE CRYPTIC VIRUS 1

1. DESCRIPTION

Main synonyms: None

Main symptoms: None observed

Agent: The genome of Grapevine cryptic virus 1 (GCV-1), a putative new species of the genus *Alphacryptovirus* consists of two double-stranded RNA molecules. RNA-1 (1,588 bp) encodes the RNA-dependent RNA polymerase whereas RNA-2 codes for the coat protein.

Transmission: With plant cryptoviruses there is no graft transmission and apparently no cell-to-cell transport, except at cell division; seed transmission is the only known mode for the transmission of alphacryptoviruses. Whether the same occurs with GCV-1 has not been ascertained.

Varietal susceptibility: No information.

Geographical distribution: Reported from the USA (Mississippi).

Detection: No information.

Control: No information.

2. HISTORICAL REVIEW

2009 **Sabanadzovic**: A sketchy report of a field survey carried out in 2007-2008 in south eastern USA.

2012 **Sabanadzovic and Abou Ghanem-Sabanadzovic**: Molecular characterization of GCV-1.

3. REFERENCES

Sabanadzovic S., 2009. Viruses of native *Vitis* germplasm in the southestern United States. *Extended Abstracts 16th Meeting of ICVG, Dijon, France*: 32-35

Sabanadzovic S., Abou Ghanem-Sabanadzovic N., 2012. Molecular characterization of two dsRNA viruses in native *Vitis* spp. *Proceedings 17th Congress of ICVG, Davis, USA*: 110-111.

SUMMER GRAPE LATENT VIRUS

1. DESCRIPTION

Main synonyms: None

Main symptoms: None observed

Agent: The genome of Summer Grape latent virus (SGLV), a putative new member of the family *Reoviridae*, subfamily *Spinareovirinae*, consists of 10 double-stranded RNA segments ranging from 3.5 kbp (segment 1) to 1.1 kbp (segment 10). All segments are monocistronic except for the one encoding the putative RNA-dependent RNA polymerase and for segment 10.

Transmission: All genomic segments contain conserved terminal sequences identical to those reported for Raspberry latent virus (RpLV), an aphid-transmitted reovirus from the Pacific northwest of the USA. Whether this may indicate aphid-transmission remains to be ascertained.

Varietal susceptibility: Detected in *Vitis aestivalis* (summer grape) but not *Vitis vinifera.*

Geographical distribution: Reported from the USA (Mississippi).

Detection: No information.

Control: No information.

2. HISTORICAL REVIEW

2009 **Sabanadzovic**: A sketchy report of a field survey carried out in 2007-2008 in south eastern USA.

2012 **Sabanadzovic and Abou Ghanem-Sabanadzovic**: Molecular characterizarìtion of SGLV.

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G. TOMBUSVIRUSES

PETUNIA ASTEROID MOSAIC VIRUS (PAMV)

1. DESCRIPTION

Main synonyms: Cherry strain of *Tomato bushy stunt virus* (TBSV-Ch)

Main symptoms: Unknown as the virus was only found in mixture with others.

Agent: PAMV is a member of the genus *Tombusvirus*, family *Tombusviridae.* Virus particles are isometric, *ca.* 30 nm in diameter sedimenting as a single component at 134S and with buoyant density in caesium chloride of 1.35 g/cm^3. The genome is a single-stranded positive-sense RNA 4.7 kb in size with the following base composition: 28% G; 27% A; 22% C; 23% U.

Transmission: Natural transmission mechanism not ultimately ascertained. The virus, however, occurs in surface waters (rivers, ditches and drainage canals), is released in the soil from the roots of infected plants, thus a direct acquisition through the soil without the intervention of a soil-borne fungal vector is likely.

Varietal susceptibility: No information.

Geographical distribution: Reported from Germany (grapevine and surface waters), Italy (grapevine, petunia, pepper, several weeds), former Czechoslovakia (grapevine, cherry, plum, hop), Switzerland, United Kingdom, former Yugoslavia, Canada (cherry).

Detection: Serologically by gel double-diffusion and ELISA.

Control: No information

2. HISTORICAL REVIEW

1957 **Lovisolo**: Description of *Petunia asteroid mosaic virus* (PAMV)

1965 **Lovisolo** *et al.*: PAMV is a soil-borne virus released from the roots of infected plants and likely acquired without the intervention of a vector.

1967 **Bercks**: First identification of PAMV in grapevines.

1967 **Ambrosino** *et al.*: Chemical and physico-chemical characterization of PAMV.

1976 **Novak and Lanzova**: Identification of PAMV in grapevines with yellow mottling of the leaves.

1976 **Dias H.F.** (in **Davidson and Allen, 1976**): The cherry strain of TBSV (= PAMV) in the grapevine in Canada.

1981 **Martelli**: Review on tombusviruses as agents of plant diseases.

1989 **Koenig** *et al.*: PAMV detected in ditches and drainage canals in a German grapevine-growing area.

1996 **Brunt**: Review of PAMV properties.

2004 **Koenig** *et al.*: PAMV isolated from surface waters in the Netherlands. The cherry strain of *Tomato bushy stunt virus* is indistinguishable from PAMV. Complete nucleotide sequence of the coat protein gene.

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Lovisolo O., 1957. Petunia, nuovo ospite del virus del rechitismo cespuglioso del pomodoro. *Bolletino della Stazione di Patologia Vegetale di Roma* **14**: 103-112.

Lovisolo O., Bode O., Voelk J., 1965. Preliminary studies on the soil trasmission of Petunia asteroid mosaic virus (= Petunia strain of Tomato bushy stunt virus). *Phytopathologische Zeitschrift* **53**: 323-342.

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GRAPEVINE ALGERIAN LATENT VIRUS (GALV)

1. DESCRIPTION

Main synonyms: None

Main symptoms: *Grapevine Algerian latent virus* (GALV) was recovered by mechanical inoculation along with *Grapevine fanleaf virus* (GFLV) from a grapevine of unknown cultivar growing in a vineyard of the Mascara hills (western Algeria). The vine showed symptoms of yellow mosaic that were attributed to GFLV. The virus, which was thought to induce symptomless infections in *Vitis vinifera*, is symptomatic in nipplefruit (*Solanum mammosum*) in which it induces mosaic and severe deformation of the leaves, and in statice (*Limonium sinuatum*), that shows chlorotic spotting of the leaves, stunting and dwarfing.

Agent: GALV is a member of the genus *Tombusvirus*, family *Tombusviridae.* Virus particles are isometric, *ca.* 30 nm in diameter and sediment as a single component at 128S and with buoyant density in caesium chloride of 1.34 g/cm^3. The genome is a single-stranded positive-sense RNA 4,731 nucleotide in size, that comprises five ORFs encoding in the 5' → 3' direction the replication-associated proteins, the coat protein, movement protein and silencing suppressor. The virus is serologically related to various extents with *Moroccan pepper virus* (MPV), *Eggplant mottled crinkle virus* (EMCV), and *Pelargonium leaf curl virus* (PLCV). GALV is one of the two tombusviruses (*Neckar river virus*, being the other) that induce vesiculation of three different organelles (peroxisomes, mitochondria and chloroplasts) leading to the formation of cytopathic structures known as "multivesicular bodies". A GALV-based virus-induced gene silencing (VIGS) vector has been developed which, following agroinfection, was able to replicate and spread systemically in *Vitis vinifera* cultivars and *Vitis riparia.*

Transmission: Mechanical transmission of the grapevine and the nipplefruit isolates to grapevine seedlings have failed. Not so the above-mentioned GALV-based vector. Natural transmission mechanism unknown. The virus, however, occurs in surface and ground waters, thus it is likely that direct acquisition through the soil may take place without the intervention of a soil-borne fungal vector.

Varietal susceptibility: No information with reference to *Vitis.* The VIGS vector apparently induces mild foliar symptoms in agroinfected vines. The natural host range, comprises also nipplefruit, statice, and pear.

Geographical distribution: Besides Algeria, records exist from Japan (nipplefruit, statice), Germany (surface waters), the Netherlands (ground waters) and Italy (surface waters).

Detection: Serologically by gel double-diffusion and ELISA and molecularly by RT-PCR with virus-specific primers

Control: No information

2. HISTORICAL REVIEW

1987 **Gallitelli** *et al.*: Description and partial characterization of *Grapevine Algerian latent virus* (GALV) (reported in 1987, published in 1989)

1987 **Russo** *et al.*: Vesiculated peroxisomes, mitochondria and chloroplasts are present in cells of GALV-infected *Chenopodiun quinoa.*

1990 **Cannizzaro** *et al.*: GALV in river waters in Sicily (southern Italy).

2002 **Russo**: Nucleotide sequence of coat protein gene of GALV.

2004 **Koenig** *et al.*: GALV isolated from ground waters in the Netherland and from surface waters in Germany.

2006 **Ohki** *et al.*: Isolation of GALV from symptomatic nipplefruit (*Solanum mammosum*) in Japan and complete sequencing of its genome.

2009 **Fujinaga** *et al.*: Isolation of GALV from symptomatic statice (*Limonium sinuatum*) in Japan.

2013 **Lovato** *et al.*: Construction of an infectious VIGS vector based on GALV.

2014 **Rubino**: Complete sequence of the grapevine isolate of GALV .

2014 **Rubino** *et al.*: Review paper on the origin, structure and function of tombusvirus induced-multivesicular bodies

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H. POTYVIRUSES

Every so often, papers are published on the presence and isolation of potyviruses from grapevines. Such records come from Germany, Israel, Japan and the USA. In all cases, the viruses have not been identified, except for a record from Mississippi, which substantiated the presence of the "peanut stripe" strain of *Bean common mosaic virus* (BCMV) in muscadine grapes. It is worth noting, however, that potyvirus sequences were detected by dot-blot hybridization in leafroll-diseased vines in Israel and that, again in Israel, it was discovered that sequences homologous to that of the coat protein of *Potato virus Y* (PVY) are contained in the genome of *V. vinifera* cv. Superior. The suggestion was that a nonhomologous recombination of a potyviral RNA with RNA of a retrotransposable element took place at some point in grapevine evolution. These latter findings are indeed of scientific interest but do not solve the problem of whether PVY occurs in grapevines in the form of an infectious disease-inducing entity.

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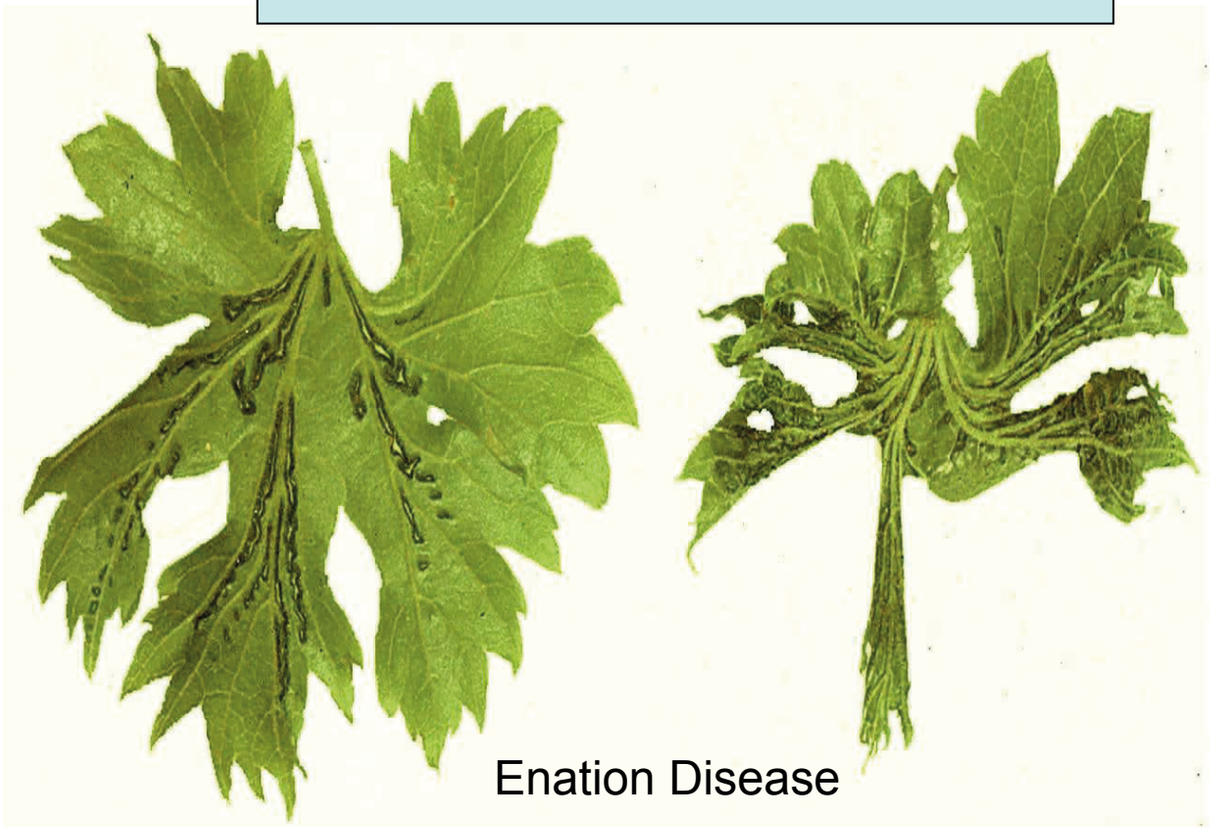
Vein mosaic

VIRUS-LIKE DISEASES



Enation Disease

VIRUS-LIKE DISEASES

Several latent or semi-latent grapevine diseases are known, some of which have a clear-cut detrimental effect on the crop. All persist in propagative material and are transmitted by grafting. Their agents are still unknown, but some are heat-labile and can be eliminated by heat therapy.

ENATION DISEASE

1. DESCRIPTION.

Enation disease of grapevine is one of the oldest known disorders of European grapes, its description dating back to the late 1800s

Main synonyms: Enationenkrankheit der Rebe (Germ.), maladie des énations (Fr.), malattia delle enazioni, omeoplasie crestiformi (Ital.).

Main symptoms: Affected vines show a delayed opening of the buds and a slow growth of the shoots in the spring, which gives a bushy aspect to the plant. Later in the year, growth tends to become normal again. Enations develop mostly on the underside of the leaves at the base of the shoots. They are outgrowths 2-3 mm high and 3-5 mm long or more, which appear more or less parallel to the main veins. Basal leaves, whether they bear enations or not, are often misshapen, with a fanlike aspect and abnormal indentation. They are often thicker than normal, with prominent veins. Severely affected leaves drop prematurely. The basal internodes are short, irregular and misshapen, and often show longitudinal cracks between the nodes. Leaves developed later in the season are usually normal. The crop can drastically reduced (up to about 50%, according to the cultivar) and is of poor quality. Symptom expression varies year by year, apparently in relation with climatic conditions. The disease has been reported from many European and extra-European countries

Agent: The aetiology of enation disease is still unknown. Graft transmission suggests that it is a virus disease. The frequent occurrence of *Grapevine fanleaf virus* in enation-bearing vines supported, in the past, the hypothesis that enation disease could be due to a severe strain of this virus. This hypothesis, however, has now been dismissed. No specific virus sequences were found in cDNA libraries from deep-sequenced vines with enations. However, micro RNAs (vvi-miRNAs) analysis in enation-showing leaf tissues disclosed an increase of miR166, which controls leaf morphogenesis. This finding suggests that the development of enations is a teratological phenomenon which, however, contrasts with the positive, though erratic, transmission by grafting.

Transmission: By vegetative propagation. The transmission by graft is erratic. The infectious agent of the disease is carried in the budwood.

Varietal susceptibility and sensitivity: Little information available. Symptoms have been observed on many *V. vinifera* cultivars, among which Panse Precoce, Primus, Italia, Riesling, Grenache and Tokay show the most severe reactions.

Geographical distribution: Likely worldwide. Records come from Europe, North America (California), North (Tunisia) and South Africa, Latin America (Venezuela), Australia and New Zealand.

Detection: Observation of symptoms in the field and indexing on LN 33. However, symptom expression is variable in successive years and graft transmission rate is very low. The absence of symptoms does not necessarily mean that vines are healthy.

Control: No information. Use of material propagated from symptomless vines does not guarantee freedom form disease.

2. HISTORICAL REVIEW.

1891 **Buchenau**: First detailed description of enation disease of grapevine from Germany.

1937 **Gigante**: Study of histological and cytological aspects of enations.

1954 **Hewitt**: Enations symptoms in California. The disease is perpetuated by vegetative propagation, and is probably due to a virus-like agent, but attempts to transmit it by graft or mechanical inoculation failed.

1966 **Graniti** *et al.*: Detailed description of macroscopic and microscopic symptoms of enation disease.

Unsuccessful attempts to transmit the disease by grafting. There is some evidence that enation is carried in the rootstocks. Only GFLV recovered by mechanical inoculation to herbaceous hosts. The conclusion is that the disease is probably of European origin, and, possibly, caused by a virus. The role of GFLV in disesase aetiology, if any, requires further investigations.

1966 **Refatti**: Hypothesis of a correlation between fanleaf and enation disease.

1966 **Martelli** *et al.*: Successful transmission of enation disease from diseased to healthy grapevine by graft strongly supports the hypothesis of a viral origin.

1968 **Brückbauer**: Description of symptoms of enation in Germany and confirmation of graft transmission of its agent.

1970 **Graniti and Martelli**: Review paper on enation. The authors discuss the hypothesis that enation is caused by a strain of GFLV but report the observations made in Australia where no GFLV was recovered from enation-affected vines.

1970 **McGechan**: Enation disease in Australia.

1971 **Tekinel** *et al.*: Enation disease in Turkey.

1973 **Hevin** *et al.*: Enation disease in France.

1975 **Pozdena** *et al.*: Enation disease in Czechoslovakia.

1978 **Avgelis and Xafis**: Enation disease in Greece.

1979 **Prota and Garau**: Enation disease found in Sardinia. In the vineyards under observation, the proportion of diseased vines was highest in cv. Malvasia (10.5%) and lowest in cv. Vernaccina (1.5%). The mean yield loss of diseased vines ranged from 17.4 to 48.3%. Confirmation of graft transmissibility of the disease.

1980 **Marinesku and Bondarchuk**: Enation disease in Moldova.

1980 **Brückbauer**: Influence of enation disease on growth and yield of grapevine in West Germany.

1981 **Prota** *et al.*: More data on the effects of enation on the yield of cv. Italia in Sardinia. Enation-affected vines produced less than 50% of the yield of healthy plants, but diseased vines which had not shown enation symptoms for several years had almost normal yields.

1983 **Nieder**: Enation disease in Austria.

1989 **Garau** *et al.*: Graft transmission trials of enation disease have shown that LN 33 is the most sensitive and reliable indicator. However, symptom expression rate does not exceed 30%.

1996 **Credi**: Enation diseasae affects the vegetative vigour of cv. Trebbiano romagnolo and reduces the yield from 13% to 23% according to the severity of symptom expression.

1997 **Padilla** *et al.*: Enation disease in Spain.

1997 **Chabbouh and Savino**: Enation disease in Tunisia.

2012 **Chiumenti** *et al.*: Deep sequencing of cDNA libraries from vines affected by enation disease failed to identify sequences of any unkown virus that could be associated with this disorder.

2013 **Chiumenti** *et al.*: Data of 2012 confirmed. However, micro RNAs (vvi-miRNAs) in enation-showing leaf tissues showed an increase of miR166 which controls leaf morphogenesis.

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Garau R., Prota U., Cugusi M., 1989. Studies on reproduction of enation symptoms by grafting in Sardinia. *Proceedings 9th Meeting of ICVG, Kiryat Anavim, Israel*: 203-206.

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VEIN MOSAIC

Main synonyms: Mosaïque des nervures (Fr.), Adernmosaik (Germ.), Mosaico delle nervature (Ital.).

1. DESCRIPTION.

The symptoms of vein mosaic have been confused for some time with those of fanleaf/yellow mosaic. However, when GFLV transmission to herbaceous hosts became possible, it became clear that vein mosaic is not caused by this virus. This disease is widespread, probably throughout the world. A similar disease has been reported in Australia under the name of summer mottle. Vein mosaic has low economic relevance.

Main symptoms: Pale green mosaic affecting mostly the tissues adjacent to the main veins or the smaller ones, producing often a vein banding effect. In the most sensitive cultivars, areas of the leaf blade may become necrotic, but these necroses do not affect the veins as in the case of vein necrosis. Symptom expression seems to depend on climatic conditions.

Agent: Unknown. Mycoplasma-like organisms were supposed to be the cause of vein mosaic, but this hypothesis has not been confirmed.

Transmission: By grafting and vegetative propagation. No vector known.

Varietal susceptibility and sensitivity: *Vitis riparia* Gloire de Montpellier and LN 33 are both sensitive, but the former is a more reliable indicator. Several *V. vinifera* cultivars show symptoms (Syrah, Servant, Viognier, Chardonnay, Alphonse Lavallée, Muscat de Hambourg, Pearl of Csaba) whereas others (Chasselas, Pinot, Gamay) are less reactive.

Geographical distribution: Reported from several European countries, Syria, North (California) and South America (Brazil), and New Zealand.

Detection: Indexing with *V. riparia* Gloire de Montpellier.

Control: Use of indexed material. The disease can be eliminated by heat therapy.

2. HISTORICAL REVIEW.

1966 **Vuittenez** *et al.*: Observation of a type of mosaic of grapevines which appears to be independent of fanleaf virus.

1973 **Legin and Vuittenez**: Description of vein mosaic. Comparison of symptoms of fleck, vein mosaic and vein necrosis.

1973 **Pop**: Vein mosaic in Romania.

1976 **Marinesku and Bondarchuk**: Vein mosaic in Moldova.

1973 **Saric and Hranuelli**: Vein mosaic in Croatia.

1973 **Samonina** *et al.*: Vein mosaic in URSS.

1978 **Krake and Woodham**: Description in Australia of a systemic mottling syndrome which is expressed during summer on the leaves of some varieties, in the absence of any detectable virus. Symptoms are very similar to those of vein mosaic in Europe.

1979 **Abracheva**: Vein mosaic in Bulgaria.

1980 **Milkus** *et al.*: Vein mosaic in Ukraine.

1982 **Vuittenez and Stocky**: Electron microscope study of thin-sectioned tissues of leaves from *Vitis riparia* and *Vitis vinifera* cv. Ehrenfelser showing symptoms of vein mosaic. A number of cytological modifications primarily involving chloroplasts were observed along with the presence of bundles of filamentous structures resembling closterovirus particles. No claim is made that these putative viruses are connected with the disease.

1983 **Woodham and Krake**: Comparison of summer mottle and vein mosaic.

1985 **Kuniyuki**: Vein mosaic in Brazil.

1993 **Golino**: Vein mosaic in California.

2004 **Bonfiglioli:** Vein mosaic in New Zealand.

2006 **Mslmanieh** *et al.*: Vein mosaic in Syria.

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Pop I.V., 1973. Grapevine vein mosaic. *Rivista di Patologia Vegetale* (S. IV) **9**: 243-250.

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Saric A., Hranuelli T., 1977. Investigation on grapevine viruses in the SR Croatia. *Proceedings Conference on Excoriosis and Virus Diseases of Grapevine, Mostar, Yugoslavia*: 149-141.

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Vuittenez A., Stocky G., 1982. Ultrastructure de vignes infectées par deux maladies de type viral: la mosaïque des nervures, ou la "feuille rouge". *Proceedings 7th Meeting of IGCV, Niagara Falls Canada*: 191-204.

Woodham R.C., Krake L.R., 1983. A comparison of grapevine summer mottle and vein mosaic diseases. *Vitis* **22**, 247-252.

RODITIS LEAF DISCOLORATION

1. DESCRIPTION

Main synonyms: None.

Main symptoms: Symptoms are prominent in late summer and consist of yellow and/or reddish discolorations of the tissues along the veins, the interveinal areas, or variously extended sectors of the leaf blade, especially near the petiole. Leaves are deformed in correspondence of discolored sectors. Bunches are reduced in numbers, size and have low sugar content.

Agent: Symptomatic grapevines were reported to be doubly infected by GFLV and *Carnation mottle virus* (CarMV) the type species of the genus *Carmovirus*, family *Tombusviridae.* CarMV is an isometric virus 30 nm in diameter, has a monopartite RNA genome accounting for *ca.* 18% of the particle weight, with mol. wt 1.4×10^6 (4003 nt in size) and coat protein subunits of M_r 38×10^3 Da. However, according to more recent findings, GFLV may not be involved in the aetiology of the disease. By converse, *Grapevine virus B* (GVB), one of the putative agents of corky bark (rugose wood complex) has a very high association (over 60%) with diseased grapevines. It is worth noting the similarity existing between Roditis leaf discoloration and Summer mottle, a putatively viroid-induced disorder from Australia, the symptoms of both of which appear during hot weather. An unnamed DNA virus of the genus *Badnavirus* has recently been found in symptomatic vines. The agent of the disease remains still to be identified.

Transmission: No vector is known. The disease is graft-transmissible. Its natural spreading in three vineyards different from the planting site of the original record was observed between 1988 and 1992. However, diagnostic tests failed to detect GFLV and CarMV in symptomatic vines, suggesting that the newly observed disease differed from the formely described disorder.

Varietal susceptibility: No information.

Geographical distribution: Reported only from Greece.

Detection: Graft-transmission to *V. vinifera* cv. Mission. Viruses associated with the disease are readily transmitted by sap inoculation and can be readily detected by ELISA and molecular techniques.

Control: No information.

2. HISTORICAL REVIEW.

1989 **Rumbos and Avgelis**: Roditis leaf discoloration described in Greece. Evidence of graft-transmissibility.

1991 **Avgelis and Rumbos**: Double infection of diseased vines by GFLV and CarMV reported.

1993 **Rumbos and Avgelis**: Newly observed cases of a disease resembling very much Roditis leaf discoloration are negative for the presence of CarMV and GFLV.

1999 **Krake** *et al.*: Roditis leaf discoloration and summer mottle may be the same disease.

2006 **Avgelis** et al.: Vines affected by Roditis leaf discoloration but not the symptomless ones contain a high percentage of GVB. The nature of the disease is still obscure.

2014 **Maliogka and Katis**: A putative badnavirus found in symptomatic vines. A breakthrough in Roditis leaf discoloration aetiology?

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SUMMER MOTTLE

Summer mottle, an Australian disease, resembles in some respects the European vein mosaic and the Greek Roditis leaf discolouration Symptoms of vein mosaic develop under mild weather conditions and fade during hot weather, whereas the opposite occurs with summer mottle. Roditis leaf discolouration and summer mottle have similarities suggesting that they may be the same disease.

1. DESCRIPTION.

Main synonyms: None.

Main symptoms: Pale green to yellowish dicolourations of the tissues adjacent to the main or secondary veins, producing a feathering or banding effect. These symptoms appear in summer and persist through the autumn. Bunches of infected cvs Sideritis and Cabernet sauvignon are fewer, poorly developed and with small berries.

Agent: Unknown, suspected to be a virus or a viroid.

Transmission: No vector is known. Spread is through infected propagative material but is has also been observed between adjacent vines.

Varietal susceptibility: No grapevine tested has been immune to infection. *V. rupestris* and LN33 are infected symptomlessly. However, several European grape cultivars show symptoms.

Geographical distribution: Reported only from Australia.

Detection: Graft transmission to a number of cvs., e.g. Cabernet franc, Cabernet sauvignon, Mission, Mataro. Symptoms show on vegetative growth that develops at temperatures in excess of 30°C.

Control: Use of disease-free propagating material obtained by culture of fragmented shoot apices.

2. HISTORICAL REVIEW.

1978 **Krake and Woodham**: Description of summer mottle in Australia. Evidence that the disease is graft-transmissible.

1982 **Barlass** *et al.*: Elimination of the disease agent by culturing fragmented shoot apices.

1983 **Woodham and Krake**: Comparative graft transmission trials demonstrate that summer mottle differs from vein mosaic. Possible viroidal etiology put forward.

1999 **Krake** *et al.*: Suggestion that summer mottle and Roditis leaf discolouration are the same disease.

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Woodham R.C., Krake L.R., 1983. A comparison of grapevine summer mottle and vein mosaic diseases. *Vitis* **22**: 247-252.

VIROID
(Yellow speckle)

VIROIDS

Viroids, the non coding genomes, are subviral pathogerns endowed with autonomous replication in their hosts. They are made up of a non encapsidated circular RNA of 246-375 nts, a size much smaller than that the smallest viral genome. Like viruses, viroids are classified in families, genera and species. Two families are known, *Pospiviroideae* and *Avsunviroideae* whose significant discriminating traits are the presence of a central conserved region in the secondary structure and nuclear replication (*Pospiviroideae*) or a branched secondary structure lacking the central conserved region, presence of ribozymes, and plastidial replication (*Avsunviroideae*). Five grapevine-infecting viroids are known, all of which belong in the family *Pospiviroideae: Grapevine yellow speckle viroid 1* (GYSVd-1), *Grapevine yellow speckle viroid 2* (GYSVd-2), *Australian grapevine viroid* (AGVd), *Hop stunt viroid* grapevine strain (HSVd-g), *Citrus exocortis viroid* grapevine strain (CEVd-g). Only GYSVd-1 and GYSVd-2 are pathogenic, inducing a disease called yellow speckle. Based on sequence variations and possible symptom-inducing abilities GYSVd-1 populations have been classified in types 1, 2 and 3.

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YELLOW SPECKLE

1. DESCRIPTION.

Main synonyms: Moucheture jaune (Fr.), picchiettatura gialla (Ital.), Gelbsprenkelung der Rebe (Germ.).

Main symptoms: Few to many minute chrome yellow spots or flecks scattered over the leaf surface, or gathering along the main veins to give a vein banding pattern. These symptoms appear in the height of summer on a limited number of mature leaves and persist for the rest of the vegetative season. The symptomatology varies depending on the cultivar, plant age, climatic conditions, and perhaps the type of infecting viroidal sequence variant. Very often, infected vines are symptomless or show symptoms erratically. Vein banding, a disease characterized by chrome yellow flecks localized along the main veins of mature leaves and progressing into the interveinal areas, thought to be elicited by a specific strain of GFLV, was demonstrated to be caused by a co-infection by yellow speckle viroids and GFLV. Sometimes,vein banding-like symptoms can be observed in vines infected only by yellow speckle viroids.

Agents: Two distinct viroids, GYSVd-1 and GYSVd -2 cause the disease individually or in combination. GYSVd-1 and GYSVd-2 are made up of 366 and 363 nucleotides (nt), respectively and belong in the genus *Apscaviroid.* Both these viroids were first isolated in Australia, from cvs Cabernet franc and Kyoto vines with yellow speckle symptoms. Neither of them is able to replicate in herbaceous hosts but both were succesfully inoculated to grapevine seedlings reproducing the yellow speckle syndrome. GYSVd-1 and GYSV-2 have a worldwide distribution. More recently a new putative viroid species denoted Grapevine yellow speckle viroid 3 (GYSVd-3) has been described.

The three additional viroids that have been detected in grapevines (HSVd-g, CEVd-g, and AGVd) are not associated with any specific symptomatology, the same as a fourth circular RNA [Grapevine hammerhead viroid-like RNA (GHVd)] whose viroidal nature is suspected but not yet proven.

AGVd, a member of the genus *Apscaviroid,* has a genome 369 nt in size. It was isolated in Australia from a grapevine that contained also other viroids and was distinguished from these because it replicated in cucumber and tomato. AGVd has been reported from Australia, USA, Tunisia, Iran, China, and Italy.

HSVd-g, the type species of the genus *Hostuviroid*, has a genome 297 nt in size. It was first detected in Japan and transmitted to cucumber and grapevine seedlings in which, however, it did not induce symptoms. Interestingly, phylogenetic analysis of hop and grapevine isolates of HSVd has provided evidence that the viroid that causes hop stunt disease in Japan is a variant of HSVd-g. The suggestion is that HSVd moved from grapevine to hop probably 50-60 ago in the Nagano and/or Fukushima prefectures in which it is not uncommon to find hop plantations next to vineyards. HSVd-g has been recorded from Australia, Europe, North and South America, and may have a worldwide distribution.

CEVd-g, a member of the genus *Pospiviroid*, has a genome 369 nt in size. It was first recoverd in Spain from symptomless grapevines. Although CEVd is present in most, if not all citrus-growing countries, its grapevine strain has only been recorded from Spain, Australia and the USA.

GHVd, is a viroid-like cicular RNA 375 nt in length with no significant similarity with any of the viroidal sequences from database, but possessing a hammerhead ribozyme and a highly branched secondary structure. GHVd was identified in a cv. Pinot noir vine from northern Italy.

Transmission: No vector is known. Natural dissemination takes place by mechanical inoculation through surface-contaminated cutting tools during management operations, grafting, and distribution of infected propagating material. This latter way of dissemination has been considered as more efficient and frequent than mechanical transmission. Experimental transmission through dodder is possible. Seed transmission has been demostrated for GYSVd-1, GYSVd-2, CEVd-g and AGVd.

Varietal susceptibility: All *Vitis* species, hybrids and cultivars appear to be susceptible. In the great majority of grapevine germplasm infection is latent.

Geographical distribution: Worldwide. Regardless of the grape-growing country, tested vines are infected by one or more viroids.

Detection: Some viroids can be transmitted mechanically to herbaceous hosts but this is not an efficient detection method. Polyacrylamide gel electrophoresis has been used extensively before the advent of nucleic acid-based assays (molecular hybridization with viroid-specific ptobes or with polyriboprobes, single-step and multiplex RT-PCR) which constitute far better detection and identification tools.

Control: Use of viroid-free propagative material obtained by meristem tip culture or somatic embryogenesis.

2. HISTORICAL REVIEW.

1972 **Taylor and Woodham**: First description of yellow speckle as a graft transmissible disease separate from chromogenic disorders induced by grapevine fanleaf virus (GFLV).

1975 **Mink and Parsons**: Yellow speckle can be detected by growing vines for 2-3 weeks at 32°C under continuous illumination.

1978 **Abracheva** *et al.*: A disease of cv. Rcatzitelli resembling yellow speckle reported from Bulgaria.

1982 **Barlass** *et al.*: Yellow speckle eliminated by *in vitro* apical culture.

1982 **Woodham and Krake**: Evidence of field spread of yellow speckle.

1983 **Krake and Woodham**: Evidence that the agent of yellow speckle is implicated in the aetiology of vein banding, a disease formerly thought to be caused by a chromogenic strain of GFLV.

1983 **Woodham and Krake**: Artificial transmission of grapevine leafroll, yellow speckle and fleck through dodder. For yellow speckle, the authors consider the results as inconclusive, as the disease may have spread naturally.

1984 **Shikata** *et al.*: First recovery of a viroid from grapevines in Japan.

1985 **Sano** *et al.*: The Japanese grapevine viroid identified as a strain of Hop stunt viroid.

1985 **Flores** *et al.*: Two new viroids, one of which identified as the agent of citrus exocortis, found in grapevine accessions from Europe and California.

1985 **Prota** *et al.*: A vein banding condition of cv. Cannonau not associated with the presence of GFLV reported from Italy.

1987 **Semancik** *et al.*: Evidence that viroids are widespread in grapevines. Three different viroids found in a number of accessions in a Californian varietal collection.

1987 **Garcia Arenal** *et al.*: Reconstruction of the secondary structure of CEVd-g.

1988 **Szychowski** *et al.*: Successful mechanical transmission of viroids to grapevines.

1988 **Rezaian** *et al.*: Four viroids found in Australian grapevines. First identification of AGVd.

1988 **Koltunow and Rezaian**: Identification and sequencing of grapevine yellow speckle viroid.

1988 **Duran-Vila** *et al.*: Improvement of meristem tip culture technique for the production of viroid-free grapevines.

1989 **Martelli**: Brief review of grapevine viroid situation supporting the idea that vein banding is primarily induced by viroidal rather than GFLV infection.

1989 **Koltunow and Rezaian**: Description and sequencing of grapevine viroid 1B (later renamed Grapevine yellow speckle viroid 2).

1989 **Koltunow** *et al.*: Evidence that two related viroids (GYSVd 1 and GYSVd 2) can cause yellow speckle disease independently.

1990 **Minafra** *et al.*: A survey of viroids of grapevine in Italy. The occurence is reported of HSVd, GYSVd-1 and GYSVd-2

1990 **Rezaian**: Complete nucleotide sequencing of AGVd. Molecular evidence that this viroid originated from recombination between five different viroids among which GYSVd-1 and GYSVd-2

1991a,b **Szychowski** *et al.*: Extensive comparative analysis of grapevine accessions from California and Europe reveal a similar pattern of viroid distribution.

1991 **Semancik and Szychowski**: There are two classes of grapevine viroids:

(i) apparent viroids, which can readily be isolated directly from grapevines;

(ii) enhanced viroids, which require amplification in an alternate host.

1991 **Rezaian** *at al.*: Structural analysis reveals that five distinct viroids infect commercial grapevine varieties. These viroids, according to an international agreement reached during the 10th Meeting of ICVG held in 1990 at Volos, Greece, are to be named as follows:

- Hop stunt viroid grapevine strain (HSVd-g),
- Citrus exocortis viroid grapevine strain (CEVd-g),
- Grapevine yellow speckle viroid 1 (GYSVd 1),
- Grapevine yellow speckle viroid 2 (GYSVd 2) and
- Australian grapevine viroid (AGVd).

1993 **Kyriakopoulou** *et al.*: HSVd and GYSVd in Greece.

1996 **Wang *et al.***: First record of grapevine viroids in China.

1996 **Polivka** *et al.*: Mutants of GYSVd-1 with altered hairpin I.

1998 **Szychowski** *et al.*: GYSVd-1 populations classified as types 1, 2 and 3. Based on sequence variation and possible symptom-inducing abilities.

1999 **Wan and Symons**: Transmission of GYSVd-1, GYSVd-2, CEVd-g and AGVd via grape seeds.

2001 **Sano** *et al.*: Suggestion that the viroid causing stunting in hop (HSVd) originated from grapevines, based on phylogenetical analysis of hop and grapevine isolates of this viroid

2002 **Elleuch** *et al.:* Molecular characterization of Tunisian grapevine viroid isolates.

2003 **Little and Rezaian**: Updated review of grapevine viroids.

2003 **Elleuch** *et al.*: First report of AGVd in the Mediterranean.

2003 **Matousek** *et al.*: Molecular characterizaiton of HSVd grapevine isolates from Czech Republic.

2003 **Gazel and Onelge**: CEVd and GYSVd-2 in Turkey.

2005 **Flores** *et al.*: Review of viroid-host interactions.

2007 **Guo** *et al.*: Detection of AGVd in a grapevine more than 100-year-old in China.

2007 **Li** *et al.*: Identification of GYSVd-1 and GYSVd-2 in China.

2009 **Navarro** *et al.*: First characterizarion based on deep sequencing analyses (Illumina technology) of the small interfering RNAs (21-24nt) derived from viroids (GYSVd-1 and HSVd).

2009 **Kawaguchi-Ito** *et al.*: Grapevines identified as a symptomless reservoir in which HSVd can evolve and be transmitted to hop crops to cause epidemics

2009a **Jiang** *et al.*: Characterizaiton of genetic diversity of AGVd in China.

2009b **Jiang** *et al.*: Molecular characterization of GYSVd-2.

2009c **Jiang** *et al.*: Identification of the tentative grapevine viroid species Grapevine yellow speckle viroid 3 (GYSVd-3).

2009 **Al Rwahnih** *et al.*: Identification of grapevine viroids by analysis of total plant RNA sequences using Life Sciences 454 high-throughput sequencing.

2009 **Zaki-Aghl and Izadpanah**: AGVd in Itan.

2010 **Hajizadeh *et al.***: Identification of multiple viroid infections in Iranian grapevines

2010 **Shu** *et al.:* CEVd in grapevines in China.

2011 **Owens** *et al.:* Updated classification of viroids.

2011 **Gambino** *et al.*: Efficient elimination of viroid infections from grapevines by somatic embryogenesis.

2011 **Ward** *et al.*: GYSVd-1 and HSVd in New Zealand.

2012 **Maree** *et al.*: Deep sequencing of South African vines affected by Shiraz disease reveals the presence of GYSVd-1, GYSVd-2, AGVd and HSVd.

2012 **Hajizadeh** *et al.*: Identification of a new variant of of GYSVd-1 denoted type 4.

2012 **Jiang** *et al.*: Diversity of viroid species in old grapevines from China and Japan may reflect different history of viticulture between the two countries.

2012 **Zhang** *et al.*: Simultaneous detection of four grapevine viroids by molecular hybridization using a polyriboprobe.

2012 **Wu** *et al.*: Discovery of a new viroid-like RNA in grapevine (Pinot noir) denoted Grapevine hammerhead viroid-like RNA by deep sequencing and a computaitonal algoritm.

2012 **Hajizadeh** *et al.*: Simultaneous detection of five grapevine viroids by a multiplex RT-PCR method.

2012 **Zhang** *et al.*: A phylogenetic analyses supports HSVd transmission between grapevine and stone fruits.

2012 **Navarro** *et al.*: Review of viroid pathogenicity.

2012 **Hammann and Steger** : Review on the effect of viroid-specific small RNAs.

2013 **Sahana** *et al.*: GYSVd-1 and HSVd in India.

2013 **Zaki-Aghl** *et al.:* Successful infection by the Iranian isolate of AGVd of several herbaceous hosts following mechanical or agroinoculation.

2014 **Gambino** *et al.:* GYSVd-2 and/or AGVd in Italian grapevine table cultivars (Sultanina bianca and Red Globe) grown in germplasm collections. *V. cinerea, V. coignetiae, V. aestivalis* and *V. candicans* are natural hosts of GYSVd-1 and/or HSVd.

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