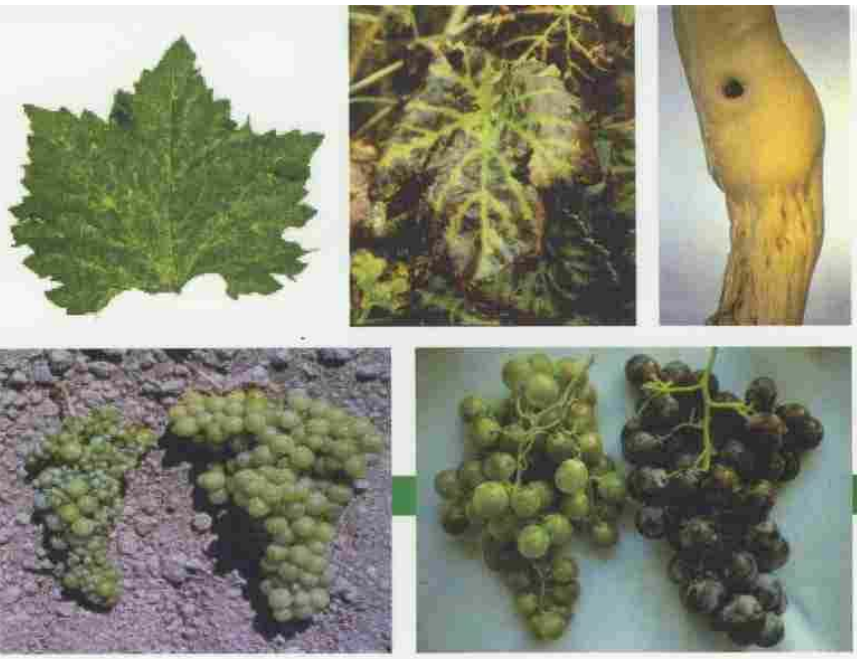

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Directory of Infectious Diseases of Grapevines

and

Viroses and Virus-like Diseases of the Grapevine: Bibliographic Report 1998-2004

CIHEAM-IAMB

Options Méditerranéennes Série B n.55

Directory of Infectious Diseases of Grapevines and Viroses and Virus-like Diseases of the Grapevine: Bibliographic Report 1998-2004

CIHEAM
Centre International de Hautes Etudes Agronomiques Méditerranéennes

Options méditerranéennes

Directeur de la publication: Bertrand Hervieu

Directory of Infectious Diseases of Grapevines and Viroses and Virus-like Diseases of the Grapevine: Bibliographic Report 1998-2004

Editors:
G.P. Martelli, E. Boudon-Padieu

2006

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Viroses and Virus-like Diseases of the Grapevine:

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PREFACE

Virus, virus-like and phytoplasma diseases of grapevines constitute a major limiting factor to the development and well-being of the world viticultural industry, and to the quality and quantity of the crop. As a whole, these diseases cause loss of vigour and often a decline of affected stocks, which reflect on the commercial value and productive life of the vineyards. Furthemore, they reduce graft compatibility of scions and rootstocks, or induce subtle debilitating effects which are difficult to percieve, except when virus-free vines are grown for comparison alongside with non-sanitized sister vines.

Improving the sanitary conditions of the industry, is therefore a goal of utmost importance to which the Mediterranean Agronomic Institute of Bari (IAM-B), taking also into account the future role of the Mediterranean as a free-trade area, is contributing with direct involvement in international research projects and through the activity the Mediterranean Network on Certification of Grapevines, that fosters coperative studies in grapevine virology.

Notwithstanding these efforts and the promoting activity of the International Council for the Study of Virus and Virus-like Diseases of the Grapevine (ICVG), it is most unfortunate that dissemination of infectious diseases continues, although the technology is now available for detection and elimination of most of the pathogens occurring in propagation material.

Scientific knowledge is nevertheless advancing rapidly and one consequence of this is the increased number of publications in specialized journals and of papers delivered during technical Meetings and Congresses. This raises the question of how to offer to those interested in a particular field the means for following with the least difficulty the research work being done in so many laboratories throughout the world and the information stemming from it.

One way of achieving this goal is to produce and make available updated accounts of the state-of-the-art of grapevine virology and comprehensive bibliographic reports. ICVG has a long-lasting tradition in these endeavours, to which IAM-B was happy to contribute, promoting the publication of the Bibliografic Report 1985-1997 on virus and virus-like diseases of the grapevine.

The present issue of Options Méditerrnéennes, hosts a new edition of the “Directory of Infectious Diseases of Grapevines” by G.P. Martelli and E. Boudon-Padieu and the latest Bibliographic Report (1998-2004) on “The Viroses and Virus-like Diseases of the Grapevine” by R. Bovey

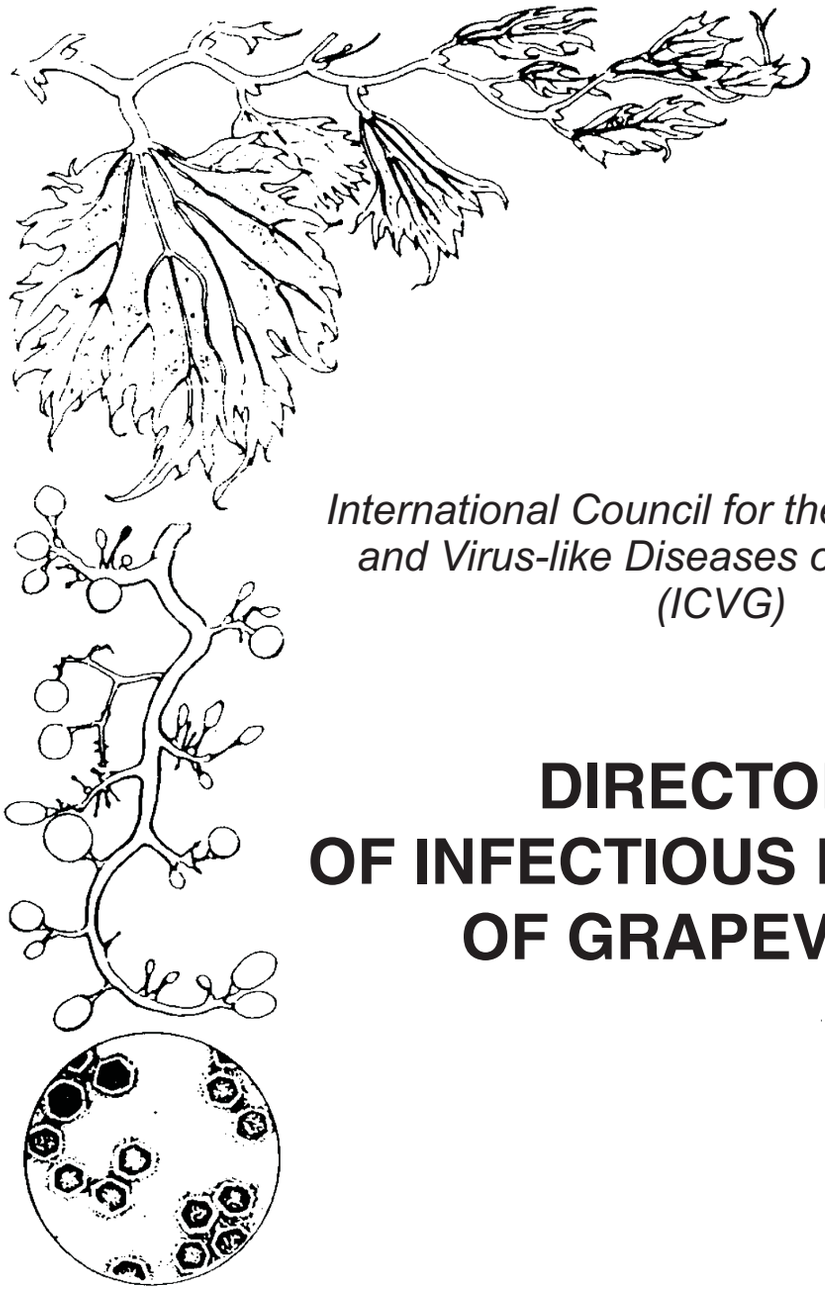
The “Directory” is a work of great thoroughness and accuracy, up to date as to the time of publication. Special care was taken in the organization of the subject matter, grouping diseases and setting them in a well thought out order, so as to produce a document which can readily be used by scientits, technicians, students, and practitioners.

As to the authors, G.P. Martelli is the President of ICVG and a widely known virologist who has much contributed to the advancement of the knowledge on grapevine viruses for the last forty years or so, whereas E. Boudon-Padieu has a long lasting experience in the study of phytoplasmas, being a recognized authority in this field.

The “Bibliographic Report” is another most precious achievement by R. Bovey, a distinguished virologist of worldwide reputation and one of the father founders of ICVG, whose Secretatiat he has admirably conducted since its very establishment in 1962.

Sincere thanks are espressed to the authors of these contributions, produced under the auspices of ICVG, whose publication IAM-B is happy to support, in the belief of rendering a good service to the scientific community and, by and large, to all those interested in viticultural matters.

Cosimo Lacirignola
Director of IAM Bari, Italy



International Council for the Study of Virus and Virus-like Diseases of the Grapevine (ICVG)

DIRECTORY OF INFECTIOUS DISEASES OF GRAPEVINES

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2006

INTRODUCTION

The grapevine (*Vitis* spp.) undoubtedly represents one of the horticultural 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 vineyards, and endangering the survival 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, that has been especially active at the international scale from the late 1950's onwards.

The increased attention paid to grapevine virological problems and the like, has produced an impressive series of papers which now number about 5,400. The papers up to 2004 are listed and commented upon 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., W.B. Hewitt and R. Bovey, 1972. Les virus de la vigne. Bibliographie de 1965-1970. *Vitis* **11**, 303-324,

Hewitt W.B. and R. Bovey, 1979. The viroses and virus-like diseases of the grapevine. A bibliographic report 1971-1978. *Vitis* **18**, 316-376,

Bovey R. and G.P. Martelli, 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. A bibliographic report 1985-1997. *Options Méditerranéenes,* **29** (Series B, 3rd part), 10-172.

Bovey R., 2006. The viroses and virus-like diseases of the grapevine. A bibliographic report 1998-2004. *Options Méditerranéenes,* **xx** (Series B, 3rd part), 205-279.

which were 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 organization for promoting research on grapevine virology and favouring the exchange of information among students. Since its foundation, ICVG has met regularly every 3 to 4 years, its 14th Conference having taken place in Italy in 2003 (Bovey and Gugerli, 2003).

Bovey R. and P. Gugerli, 2003. A short history of ICVG. *Extended Abstracts 14th Meeting of ICVG, Locorotondo 2003*, 1-2.

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 and certification programmes.

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

The International Council for the Study of Virus and Virus-like 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.

(issued and 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.

(issued and approved in 2003 at the 14th ICVG Meeting, Locorotondo, Italy)

The Proceedings of all the international ICVG Conferences have been published *in extenso* or, lately, as Extended Abstracts. They represent a most valuable source of information. In addition, the virological problems of grapevines have been extensively treated and illustrated in a number of books and major review articles:

Uyemoto J.K, G.P. Martelli, R.C. Woodham, A.C. Goheen and H.F. Dias, 1978. Grapevine (*Vitis*) virus and virus-like diseases. Plant Virus Slide Series, Set 1 (O.W. Barnett and S.A. Tolin, eds) Clemson University, Clemson, 100 slides, 29 pp. (a revised edition by J.K. Uyemoto, G.P. Martelli and A. Rowhani will be published in 2005 in the series APS Plant Virus Image CD-ROM, Grape Section, under the name of Grapevine Viruses, Virus-like Diseases and Other Disorders).

Bovey R., W. Gärtel, W.B. Hewitt, G.P. Martelli and A. Vuittenez, 1980. Virus and Virus-like Diseases of Grapevines. Editions Payot, Lausanne, 181 pp.

Pearson R.G. and A.C. Goheen, 1988. Compendium of Grape Diseases. The American Phytopathological Society Press, St. Paul, Minnesota, USA, 93 pp. (a 2nd revised edition edited by W.F. Wilcox, W.D. Gubler and J.K. Uyemoto will be published in 2005).

Frison E.A. and R. Ikin, 1991. FAO/IBPGR Technical Guidelines for the Safe Movement of Grapevine Germplasm. Food and Agriculture Organization of the United Nations, Rome /International Board for Plant Genetic Resources, Rome, 54 pp.

Martelli G.P. (ed.), 1993. Detection and Diagnosis of Graft-transmissible Diseases of Grapevines. FAO Publication Division, Rome, 263 pp.

Walter B. and G.P. Martelli, 1996. Sélection sanitaire de la vigne: sélection sanitaire et sélection pomologique. Influence des viroses et qualité. 1ere partie: Effets des viroses sur la culture de la vigne et ses produits. *Bulletin de l'OIV* **69**, 945-971.

Walter B. and G.P. Martelli, 1997. Sélection sanitaire de la vigne: sélection sanitaire et sélection pomologique. Influence des viroses et qualité. 2ere partie: Sélection sanitaire, sélection pomologique. *Bulletin de l'OIV* **70**, 5-23.

Walter B. (ed), 1997. Sanitary selection of the grapevine. Protocols for detection of viruses and virus-like diseases: Les Colloques, n° 86, INRA Editions, Paris, 225 pp.

Martelli G.P. and B. Walter, 1998. Virus certification of grapevines. In: Plant Virus Disease Control (A. Hadidi, R.K. Khetarpal, H. Koganezawa, eds.), 261-276. American Phytopathological Society Press, St. Paul.

Krake L.R., N.S. Scott, M.A. Rezaian and R.H. Taylor, 1999. Graft-transmissible Diseases of Grapevines. CSIRO Publishing, Collingwood,137 pp.

Walter B., E. Boudon-Padieu and M. Ridé, 2000. Maladies à Virus, bactéries et phytoplasmes de la Vigne. Editions Féret, Bordeaux, 192 pp.

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.

At the 14th ICVG Meeting, the Steering Committee of ICGV decided to update the Directory and to entrust this task to G.P. Martelli and E. Boudon-Padieu.

The authors hope that this endeavour may serve as a useful guideline and working tool for both experienced researchers and those who are now approaching the intriguing but intricate field of grapevine virology.

They express their deep gratitude to Prof. M. Hamze and Mr. B. Hervieu, Chairman of the Board of Directors and Secretary General, respectively, of the Centre International des Hautes Etudes Agronomiques Méditerranéennes, Paris, and to Dr. C. Lacirignola, Director of the Mediterrenean Agronomic Institute of Bari for supporting the publication of this work.

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INFECTIOUS AGENTS OF GRAPEVINES

More than 70 infectious agents among viruses (58), 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.

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

FAMILY	GENUS	SPECIES
A. Viruses belonging to genera included into families		
BROMOVIRIDAE	*Alfamovirus*	*Alfalfa mosaic virus* (AMV)
	Cucumovirus	*Cucumber mosaic virus* (CMV)
	Ilarvirus	Grapevine line pattern virus (GLPV)
		Grapevine angular mosaic virus (GAMoV)
BUNYAVIRIDAE	*Tospovirus*	*Tomato spotted wilt virus* (TSWV)
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) *Grapevine leafroll-associated virus 5* (GLRaV-5) Grapevine leafroll-associated virus 6 (GLRaV-6) Grapevine leafroll-associated virus 7 (GLRaV-7) Grapevine leafroll-associated virus 8 (GLRaV-8) Grapevine leafroll-associated virus 9 (GLRaV-9)
Two new putative ampeloviruses are being characterized in France and the USA		
COMOVIRIDAE	*Fabavirus*	*Broadbean wilt virus* (BBWV)
	Nepovirus	*Artichoke italian latent virus* (AILV) *Arabis mosaic virus* (ArMV) *Blueberry leaf mottle virus* (BBLMV) *Cherry leafroll virus* (CLRV) *Grapevine Bulgarian latent virus* (GBLV) Grapevine Anatolian ringspot virus (GARSV) Grapevine deformation virus (GDefV) *Grapevine chrome mosaic virus* (GCMV) *Grapevine fanleaf virus* (GFLV) *Grapevine Tunisian ringspot virus* (GTRV) *Peach rosette mosaic virus* (PRMV) *Raspberry ringspot virus* (RpRV) *Tobacco ringspot virus* (TRSV) *Tomato ringspot virus* (ToRSV) *Tomato blackring virus* (TBRV)
FLEXIVIRIDAE	*Foveavirus*	*Grapevine rupestris stem pitting-associated virus* (GRSPaV)

Potexvirus	*Potato virus X* (PVX)	
	Trichovirus	*Grapevine berry inner necrosis virus* (GINV)
	Vitivirus	*Grapevine virus A* (GVA) *Grapevine virus* B (GVB) Grapevine virus C (GVC) *Grapevine virus D* (GVD)
TOMBUSVIRIDAE	*Carmovirus*	*Carnation mottle virus* (CarMV)
	Necrovirus	*Tobacco necrosis virus D* (TNV-D)
	Tombusvirus	*Grapevine Algerian latent virus* (GALV) *Petunia asteroid mosaic virus* (PAMV)
TYMOVIRIDAE	*Marafivirus*	*Grapevine asteroid mosaic-associated virus* (GAMaV) Grapevine redglobe virus (GRGV)
	Maculavirus	*Grapevine fleck virus* (GFkV) *Grapevine rupestris vein feathering virrus* (GRVFV)

A new putative marafivirus is being characterized in the USA

POTYVIRIDAE	*Potyvirus(?)*	Unidentified potyvirus-like virus isolated in Japan from a Russian cultivar

B. Viruses belonging to unassigned genera

	Idaeovirus	*Raspberry bushy dwarf virus* (RBDV)
	Sadwavirus	*Strawberry latent ringspot virus* (SLRSV)
Sobemovirus		*Sowbane mosaic virus* (SoMV)
	Tobamovirus	*Tobacco mosaic virus* (TMV) *Tomato mosaic virus* (ToMV)

C. Taxonomically unassigned viruses

		Unnamed filamentous Grapevine Ajinashika virus (GAgV) Grapevine stunt virus (GSV) Grapevine labile rod-shaped virus (GLRSV)

[(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: Fauquet, C.M., Mayo, M.A., Maniloff, J., Desselberger, U. and Ball, L.A. (eds), 2005. Virus Taxonomy, 8Ith Report of the International Committee on Taxonomy of Viruses. Elsevier/Academic Press, London, pp. 1258.

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 *Grapevine fanleaf virus* (GFLV). The name of this virus comes from the peculiar malformation of infected leaves, which exhibit widely open petiolar sinuses and abnormally gathered primary veins, that give 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 viruses. Tolerant cultivars produce fairly good crops whereas sensitive cultivars are severely affected, showing progressive decline, 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 were found 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 virus strains causing distortions. Leaves are variously and 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 in number, 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 rapidly and the canopy develops a normal green color.

The characterizing symptoms of "*Vein banding",* another disease sometimes occurring 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 which appear in mid to late summer in a limited number of leaves. Symptomatic leaves show little malformation. Fruit set is poor, bunches are straggly, and the yield may be much reduced. This disorder was first reported from California as a syndrome elicited by a specific strain of GFLV. More recently, however, vein banding symptoms were shown to be caused by a co-infection by *Grapevine yellow speckle viroid* and GFLV.

Trabeculae, or endocellular cordons, i.e. radial bars crossing the lumen of epidermal, parenchyma, phloem, and xylem cells, are diagnostic of grapevines infected by GFLV. These structures are readily visible 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 rather uniform and occurring as a family of minor molecular variants. Positive sense single-stranded RNA genome, consisting of two functional molecules 7342 nt (RNA-1) and 3774 nt (RNA-2) in size, encapsidated in different particles, both required for infectivity. GFLV was the first grapevine virus to be recovered by mechanical inoculation and to be thoroughly characterized physico-chemically and molecularly. A satellite RNA 1114 nt in size is associated with some virus isolates.

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 membrane proliferation, reorganization, and redistribution and are thought to be sites of viral polyprotein processing and RNA replication. Virus particles are often 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 vascular bundles, 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. 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 grapevines 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 (Vitis) 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* x *M. rotundifolia* hybrid rootstocks (e.g. O36-16) show interesting levels of field resistance to GFLV.

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 and immunocapture RT-PCR are becoming increasingly popular. RT-PCR is estimated to be four to sixfold more sensitive than ELISA. 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 greenhouses 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 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. 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 is more and more questioned for environmental reasons and is being progressively banned. Work is under way in different laboratories to create GFLV-resistant rootstocks or cultivar through traditional breeding methods or genetic transformation technology. For transformation, a number of selectable marker genes toxic to non engineered vines are used. However, 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 1000 papers dealing with fanleaf. For a comprehensive review on early observations, research and hypotheses on fanleaf, as well as on 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

1910 **Pantanelli**: Fanleaf disease can be trasmitted through the soil

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 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.

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. Report on first experiments on heat treatment of grapevine in order to eliminate 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.

(a) See references in the 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.

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. Transmission of fanleaf virus by *X. index*. Control of the vector 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 showed that Californian and Italian GFLV isolates are the same. Reproduction of fanleaf symptoms in mechanically inoculated grapevine seedlings

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 and shoot extremities 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 fanleaf virus: bentonite flocculation test, latex test and barium sulfate test.

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

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 the moult of the nematode, 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 minutes. 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*.

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 latex test and ELISA for detecting GFLV in France. Both tests are more sensitive than mechanical inoculation to *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 in 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**: *Muscadinia rotundifolia* becomes infected by GFLV when the virus is transmitted by grafting but resists infection when transmission is by *X. index* feeding.

1983a **Bouquet**: *M. 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 etiology of vein banding.

1983 **Morris-Krsinich** *et al*.: *In vitro* translation of genomic RNAs of GFLV yields two large polyproteins (220 Kd and 125 Kd) 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 represent 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 made it possible to eliminate both viruses from the developing shoot tips (2 mm) of *in vitro* cultured 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 the variety 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. 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, RpRV, 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

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 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

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.

1994 **Walker** *et al*.: Two *Vitis vinifera* x *Muscadinia rotundifolia* rootstock hybrids (O39-16 and O43-43) grafted with Cabernet sauvignon showed a high level of tolerance to GFLV. Both became infected in the course of a 12-year trial but had no reduced crop yields, thus qualifying for use in *X. index* infested soils, O39-16 in particular, which is also resistant to phylloxera.

1995 **Brandt and Himmler**: Use of immunocapture RT-PCR for GFLV detection in host tissues.

1995 **Krastanova** *et al*.: Genetic transformation of American roostocks with the coat protein gene of GFLV for resistance induction.

1995 **Mauro** *et al.*: Genetic transformation of *Vitis vinifera* with the coat protein gene of GFLV for resistance induction.

1995 **Ritzenthaler** *et al.*: Demostration that the movement protein of GFLV is located on the intracellular tubular structures containing rows of virus particles.

1995 **Rowhani** *et al*.: Development of a GFLV detection system based on PCR analysis of immobilized virions.

1996 **Walter and Martelli**: Review article on detrimental effects of viruses on grape yields**.**

1996 **Lahogue and Boulard:** Search for genes of resistance in grapevines. Of 531 accessions of European, American, and Asian *Vitis* species inoculated by green grafting with a GFLV source, except for four, all were susceptible to the virus, including the two accessions reported as resistant by Walker and Meredith (1990).

1997 **Spielmann** *et al*.: Transformation of *Nicotiana* species and *Vitis rupestris* with different virus-derived (coat protein, replicase) and exogenous (2, 5 oligoadenylate synthase, RNase L) genes for inducing resistance to GFLV. The level of resistance obtained looks promising.

1998 **Martelli and Walter**: Review article on certification of grapevines**.**

1998 **Walker and Jin**: *V. rupestris* x *M. rotundifolia* hybrids show high resistance to *X. index* feeding. This resistance is controlled by a single dominant gene.

1999 **Gaire** *et al*.: Demonstration that a 28 kDa protein coded by GFLV RNA-2 is involved in the replication of this RNA.

1999 **Belin** *et al*.: Identification of the molecular signal accounting for the systemic spread of GFLV in infected hosts.

2000 **Naraghi-Aran**i *et al.*: Variations observed following RT-PCR and RFLP analysis of the coat protein gene of nine GFLV isolates grown in different hosts confirm the quasispecies nature of this virus.

2000 **Pinck**: A comprehensive review of the molecular aspects of GFLV genome and its replication strategy.

2000 **Pfeiffer** *et al.*: The membranous structures appressed to the nucleus of infected cells known as vacuolate-vesiculate inclusion bodies are virus factories as they are the likely site of RNA replication and processing of viral polyproteins.

2000 **Gölles** *et al*.: Successful transformation of somatic embryos of an European grape cultivar (Russalska 3) with the normal, truncated or nontranslatable coat protein gene of GFLV*.*

2001 **Belin** *et al.* : Identification of RNA2-encoded proteins in the specific transmission of GFLV by *X. index.*

2002 **Ritzenthaler** *et al.*: Identification of membranes derived from the endoplasmic reticulum as sites of GFLV replication*.*

2003 **Pfeiffer** *et al*.: Up to date account of GFLV replication strategy*.*

2003 **Fuchs**: Review article on genetic transformation of grapevines for resistance to GFLV and other pathogens.

2003 **De Luca** *et al.*: Attempts to characterize molecularly *X. index* populations by PCR-RFLP and sequencing of the ITS region.

2003 **Martelli** *et al*.: Redescription of GFLV in the AAB Descriptions of Plant Viruses.

2003 **Laporte** *et al.*: Movement protein of GFLV is transported via Golgi-derived vesicles along microtubules to specipic receptors present in plasmodesmata.

2003 **Demangeat** *et al*.: Evidence that in soil samples stored at 7 °C and 20 °C *X. index* individuals survive up to four years and remain viruliferous for at least 12 months.

2003 **Izadpanah K.** *et al*.: Detection of GFLV in *Cynodon dactylon* and *Polygonum aviculare.*

2003 **Bouyahia H**. *et al*.: Comparison of sampling methods for ELISA detection of GFLV.

2004 **Fischer and Schillberg**: Generation of recombinant single chain antibody fragments to GFLV and ArMV for resistance induction in grapevines.

2004 **Kieffer** *et al*.: Mannose and xylose proved not suitable for use as selectable marker genes for transformation of cv. Chardonnay.

2004 a **Vigne** *et al.*: Study of the pouplation structure and genetic variability of GFLV. High frequency of mixed infections by distinct molecular variants in natural virus populations and evidence for intraspecific recombination.

2004b **Vigne** *et al.*: Genetically transformed grapevines expressing the coat protein of GFLV do not assist in the emergence of viable recombinant virus strains.

2004 **Andret-Link** *et al*.: The coat protein of GFLV is the sole determinant for the specific transmission of the virus by *X. index.*

2004 **Andret-Link** *et al*.: Updated review of the biological, epidemiological and molecular properties of GFLV and of its interaction with the host.

2004 **Demangeat** *et al.:* Improved method for the detection of GFLV in single individuals of *X. index* from greenhouse rearings of field populations.

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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. Many are transmitted by longidorid nematodes (Rüdel, 1992). Serological (ELISA, ISEM) and molecular assays (hybridization, RT-PCR) are routinely used for their detection in grapevine tissues (primarily cortical scrapings from dormant canes). Mechanical transmission to herbaceous hosts or indexing on *Vitis* indicators can also be used. These viruses can readily be eliminated by heat therapy or *in vitro* meristem tip culture. Their detrimental effects to grapevine culture and products have been summari zed by Walter and Martelli (1996).

Nepoviruses, which were originally included in the Nepovirus group (Harrison and Murant, 1977) , a non-taxonomic clustering, are now classified in the genus *Nepovirus,* family *Comoviridae* (Goldbach *et al.*, 1955) and are subdivided into subgroups based on physico-chemical properties of member viruses, 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*, has now been assigned to the newly established genus *Sadwavirus* (Le Gall *et al.*, 2005)

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

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Taylor C.E and D.J.F. Brown, 1997. Nematode Vectors of Plant Viruses. CAB International, Oxon, 286 pp.

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Genus *NEPOVIRUS*

ARABIS MOSAIC VIRUS (ArMV)

1. Description

ArMV, a typical nepovirus belonging in subgroup A of the genus *Nepovirus*, 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 x 10^3. The genome is a positive sense ssRNA, consisting of two separately encapsidated molecules with Mol. wt 2.2 x 10^6 (RNA-1) and 1.95-2.1 x 10^6 (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 x 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, Bulgaria, Yugoslavia, Hungary, Romania, Turkey, Iran, Israel, Canada, USA (California), and Japan. It 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 sequenece of a small circular satelllite RNA

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 can be found in both rootstock and scion. Study of histological changes at the graft union level.

1989 **Eppler** *et al*.: ArMV recorded from 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 protien 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 engineerd with ArMV coat protein gene show different degrees of tolerance to the virus

1994 **Flak and Gangl**: ArMV recorded from Austria

1995 **Loudes** *et al*.: Evidence that ArMV has two RNA-2 molecules and 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 a ArMV source, 42 were apparently resistant.

1998 **Akbas and Erdiller:** ArMV recorded from Turkey

2000 **Goelles** *et al.* : Transgenic grapevines expressing ArMV coat protein gene

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

2004 **Pourrahim** *et al*.: ArMV identified in Iranian grapevines by mechanical transmission to herbaceous hosts and ELISA

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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 x 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 x 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 x 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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Savino V., D. Gallitelli, M. Jankulova and G.L. Rana, 1976. A comparison of four isolates of Artichoke Italian latent virus (AILV). *Phytopathologia Mediterranea* **16**, 41-50.

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. 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 sequenced only in part. Genomic RNA consists of two separately encapsidated functional molecules with Mol. wt of 2.8×10^6 (RNA-1) , accounting for 46% of the particle weight, and 2.3×10^6 (RNA-2), accounting for 41% of the particle weight. 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-2.

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.

3. References

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GRAPEVINE ANATOLIAN RINGSPOT VIRUS (GARSV)

1. Description

Grapevine Anatolian ringspot Virus (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 and RNA-2 a Mol. wt of 1.4×10^6 Da and a size of 4607 nt. Coat protein subunits have a Mr 56×10^3 Da. 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 was reported only from south-eastern Turkey. 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

3. References

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

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Gokalp K. M. Digiaro, I. Cigasr, N. Abou Ghanem-Sabanadzovic, A. De Stradis, D. Boscia and G.P. Martelli, 2003. Properties of a previously undescribed nepovirus fron south-east Anatolia. *Journal of Plant Pathology* **85**, 35-41.

GRAPEVINE BULGARIAN LATENT VIRUS (GBLV)

1. Description

Grapevine Bulgarian latent virus (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 not known. 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, B_1, and B_2). Component T is made up of empy protein shells, whereas components B_1 and B_2 contain RNA. Coat protein has a single type of subunits with M_r 54 x $10^{3.}$ The genome is a positive sense ssRNA, consisting of two separately encapsidated molecules with Mol. wt of 2.2 x 10^6 (RNA-1) and 1.95-2.1 x 10^6 (RNA-2), accounting for 39% (componet B_1) and 42% (component B_2) of the particle weight. The virus supports the replication of a satellite RNA with Mol. wt 0.5 x 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 serologically 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.

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GRAPEVINE CHROME MOSAIC VIRUS (GCMV)

1. Description

Grapevine chrome mosaic virus (GCMV) was first found in Hungary, near Lake Balaton, and was originally called Hungarian chrome mosaic virus. It has been recorded also from Czechoslovakia, Croatia and Austria. The genome is bipartite. RNA-1 has Mol. wt of 2.8×10^6, a size of 7212 nt and accounts for 40% of the particle weight. RNA-2 has Mol. wt of 1.6×10^6, a size of 4441 nt and accounts for 31% of the particle weight. The coat protein has a single type of subunits of M_r 52×10^3. Leaves of infected vines are partially or entirely bright yellow or whitish, a symptom virtually indistiguishable from GFLV-induced yellow mosaic. Affected vines lack in vigour and may decline and die. Some virus strains induce leaf deformity, double nodes and short internodes, pretty much like GFLV. However, symptomless infection may occur. The virus belongs in the same subgroup of TBRV (subgroup B) to which is distantly related serologically. Although GCMV particles have been detected by immunosorbent electron microscopy 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 pants and the rootstock 110R have been successfully transformed with the viral coat protein for induction of resistance.

2. Historical review

1966 **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 appears to be unrelated serologically to GFLV and is not transmitted by *X. index.*

1966 **Martelli:** Purification and serology of the virus isolated from Hungarian grapevines with fanleaf- and yellow mosaic-like symptoms. The virus is not serologically related 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 roostock 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.

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Taylor C. E. and D.J.F Brown, 1997. Nematode Vectors of Plant Viruses. CAB International, Oxon, 286 pp.

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*, is distantly related serologically to ArMV but not to GFLV. Particles are isometric c. 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 and RNA-2, mol. wt of 1.3×10^6 Da and a size of 3753 nt. 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 reported only from south-eastern Turkey. 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. 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

3. References

Abou Ghanem-Sabanadzovic N., S. Sabanadzovic, M. Digiaro and G.P. Martelli, 2005. Complete nucleotide sequence of RNA-2 of two Turkish nepoviruses. *Virus Genes* **30**, 335-340
Cigsar I., M. Digiaro and G.P. Martelli, 2002. Sanitary status of grapevine in south eastern and central Anatolia. *Bulletin OEPP/EPPO Bulletin* **32**, 471-475
Cigsar I., M. Digiaro, K. Gokalp, N. Abou Ghanem-Sabanadzovic, A. De Stradis, D. Boscia and G.P. Martelli, 2003. Grapevine deformation virus, a novel nepovirus from Turkey. *Journal of Plant Pathology* **85**, 35-41.

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 *c*. 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 *c*. 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.

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Ouertani R., V. Savino, A. Minafra, D. Boscia, M.A. Castellano, G.P. Martelli and N. Greco, 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 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 for it often sediments as if it were a single centrifugal component. These differences strongly suggest that the grapevine-infecting RpRSV may be a different viral species. 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 3928 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 only been found in grapevine in western Germany. Symptoms are similar to those of fanleaf. Two 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 RpBRSV 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

3. References

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Jones A.T., D.J.F. Brown, W.J. McGavin, M. Rüdel and B. Altmayer, 1994. Properties of an unusual isolate of raspberry ringspot virus from grapevine in Germany and evidence of its possibile transmission by *Paralogidorus maximus*. *Annals of Applied Biology* **124**, 283-300.

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Vuittenez A., J. Kuszala, M. Rüdel and H Brückbauer, 1970. Détection et étude selogique du virus latent des taches annulires 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

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). The virus is a definitive nepovirus species classified in subgroup A of this genus, its own subgroup. 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 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 x 10^6 (RNA-1) and 1.65 x 10^6 (RNA-2) accounting for 44% and 37% of the particle weight, respectively. RNA-1 is 7356 nt in size and contains a single open reading frame encoding a polypeptide with M_r of 254 kDa. RNA-2 is 4662 nt in size encoding a polyprotein with M_r of 150 kDa. TBRV supports the replication of a satellite RNA with Mol. wt of 0.5 x 10^6 daltons and a size of 1327 nt. TBRV produces a reduction in growth and yield, chlorotic spots, rings and lines on the leaves of recently infected plants, mottling of the older leaves, and an increase in graft failure. The vector to grapevine is *Longidorus attenuatus.* Losses are not known precisely, but they can be high. Joannes Seyve virus, known to cause severe damage to the grapevine variety Joannes Seyve in Ontario, is a strain of this virus.

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.

1970b **Stellmach**: Review paper on TBRV in grapevine.

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, Ontario 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 TBRV RNA-2

1988 **Greif** *et al*.: Nucleotide sequence of TBRV RNA-1

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

3. References

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Vuittenez A., J. Kuszala, M. Rüdel and H. Brückbauer, 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.

Genus *SADWAVIRUS*

STRAWBERRY LATENT RINGSPOT VIRUS (SLRSV)

1. Description

Strawberry latent ringspot virus (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 virus is a definitive species in the genus *Sadwavirus.* 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 x 10^3 and 27 x 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 x 10^6 (RNA-1) accounting for 38% of the particle weight, and 1.6 x 10^6 (RNA-2). RNA-2 is 3824 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 1118 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 vrises 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.

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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 and Ontario) 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 ring spots) and distorted leaves, distortion of canes, poor fruit setting, straggly and shelled clusters. In warmer climates (Maryland, California) 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 setting. 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: These viruses are all 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 t*ransmit 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 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 are useful for testing field-infected material.

Control: Use of virus-free propagating material and resistant rootstocks. Nematicidal control of vectors is possible, but 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 x 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 x 10^6 (RNA-1) and 2.15 x 10^6 (RNA-2). 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 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 'Concord' vines showing fanleaf-like symptoms, but 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

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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 crop 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 x 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 x 10^6 (RNA-1) and 2.2 x 10^6 (RNA-2) accounting for 44% and 37% of the particle weight, respectively. RNA-1 is 8004 nt in size and contains a single open reading frame encoding a polypeptide with M_r of 240 kDa. 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 from 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 some 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 seedlings from seeds taken from diseased vines proved to be infected. PRMV is seed-borne in both naturally infected dandelion (4% of infected seeldlings) and in artificially infected *C. quinoa* (90% of 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 trees 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.

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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.

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

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

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

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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 x 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 x 10^6 (RNA-1) and 1.3 x 10^6 (RNA-2), accounting for 44% and 28% of B and M particle weight, respectively. RNA-1 is 7514 nt in size and contains a single open reading frame encoding a polypeptide with M_r 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 was 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.

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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 x 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 x 10^6 (RNA-1) and 2.4 x 10^6 (RNA-2) accounting for 44% and 41 % of the particle weight, respectively. RNA-1 is 8214 nt and RNA-2 is 7273 nt in size. Both RNAs contain a single open reading frame encoding polypeptides with M_r 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 iin 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 north American 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

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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:** Record of 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.

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

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

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Uyemoto J.K., J.R. Cummins and G.S. Abawi, 1977. Virus and virus-like diseases affecting grapevines in New York vineyards. *American Journal of Enology and Viticulture* **28,** 131-136.
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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 is probably the most widespread virus disease of grapevine. Its occurrence in viticultural areas is worldwide.

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 canes as the season advances. In the most severe cases, 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) and affects negatively rooting ability, graft take and plant vigour. Also plant anatomy is affected, especially the phloem. Sieve elements are obliterated and crusheds, thus impairing 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 if the disease is eliminated by sanitation treatments.

Agents: To date, nine different viruses with filamentous particles, called grapevine leafroll-associated viruses (GLRaV), which are differentiated from one another by a progressive number, have been found in leafroll-infected vines. Other such viruses may exist. Until 1995, differentiation of GLRaVs at the species level was by Roman numerals, now is by Arabic numerals:

Grapevine leafroll-associated virus 1 (GLRaV-1)
Grapevine leafroll-associated virus 2 (GLRaV-2)
Grapevine leafroll-associated virus 3 (GLRaV-3)
Grapevine leafroll-associated virus 4 (GLRaV-4)
Grapevine leafroll-associated virus 5 (GLRaV-5)
Grapevine leafroll-associated virus 6 (GLRaV-6)
Grapevine leafroll-associated virus 7 (GLRaV-7)
Grapevine leafroll-associated virus *8* (GLRaV-8)
Grapevine leafroll-associated virus 9 (GLRaV-9)

A potyvirus isolated in Israel from leafroll-infected vines is now regarded as an occasional contaminant. All GLRaVs belong in the family *Closteroviridae,* GLRaV-2 in the genus *Closterovirus*, GLRaV-1, GLRaV-3, GLRaV-4, GLRaV-5, GLRaV-6, GLRaV-8, and GLRsV-9 in the newly established genus *Ampelovirus*, whereas GLRaV-7 is presently classified as unassigned species to the family. Virus particles 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 2200 nm according to individual viruses, the same as the size of coat protein (CP) subunits. GLRaV-2 CP has a M_r of 24 kDa, whereas the M_r 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 is a monopartite, single-stranded, positive sense RNA molecule. The genome of GLRaV-2 is 15,528 nt in size, contains nine open reading frames (ORF) and has structural organization identical to that of *Beet yellow virus* (BYV), the type member of the genus. GLRaV-3, which is the type species of the novel genus *Ampelovirus* has a genome 17,919 nt in size, contains 13 ORFs, and has structural organization differing from that of other sequenced closteroviruses. The genome of GLRaV-1 is 17,647 nt in size and contains 10 major ORFs. The genome of GLRaV-4 and GLRaV-9 are incompletely sequenced but show a structural organization compatible with that of the genus. 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. GLRaV-5 and GLRaV-9 are phylogenetically close to one another but are serologically unrelated. Regardless of whether they belong to the genus *Closterovirus* or *Amplelovirus*, GLRaVs show molecular variations which give rise to a population of strains, in agreement with the quasispecies nature of viruses. This has been ascertained experimentally for GLRaV-1, GLRaV-2 and GLRaV-3. Other GLRaVs may exist in nature as suggested by reports.

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 eitrher from peripheral vesiculation of mitochondria followed by disruption of the organelles (GLRaV-1, GLRaV-3, GLRaV-5) 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. So far, only vectors of GLRaV-1, GLRaV-3, GLRaV-5 and GLRaV-9 have been identified. GLRaV-1 is transmitted in nature by the pseudococcid mealybugs *Heliococcus bohemicus* and *Phenacoccus aceris* and the soft scale insects *Pulvinaria vitis*, *Parthenolecanium corni,* and *Neopulvinaria innumerabilis.* Mealybug vectors of GLRaV-3 are *Planococcus ficus*, *Pl. citri*, *Pseudococcus longispinus, Ps. calceolariae, Ps. maritimus, Ps. affinis, Ps. viburni* and *Ps. comstocki.* Its soft scale insects vectors are *Pulvinaria vitis* and *Neopulvinaria innumerabilis.* GLRaV-5 and GLRaV-9 are both transmitted by *Ps. longispinus.*Transmission is semipersistent and does not appear to be vector-specific. 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 an 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.

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 discriminate 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 variants which can be differentiated by the reaction of inoculated *Nicotiana* species. or 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 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 for leafroll control available. No sources of resistance are known in *V. vinifera* and there is no published information on how to protect healthy stocks from vector-mediated reinfection in the field. Introduction of transgenic resistance to GLRaV-2 and GLRaV-3 is being attempted by engineering different viral genes into rootstocks and European grape cultivars.

2. Historical review

1906 **Sannino**: Occurrence in Italy of “rossore”, a grapevine disorder similar to leafroll**.**

1924 **Ravaz and Verge**: Occurrence in France of “rougeau”, a grapevine disorder similar to leafroll

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.

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 souces 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* meristm tip culture and apex fragmentation.

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

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 also reacted 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 for ELISA and ISEM to GLRaV-1 and GLRaV-3.

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 Brasil

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* 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 rootstock, 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 ofthe 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 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 Nebbiolo clone and the quality of the must.

1997 **Faoro**: Comprehensive review of the ultrastructure of GLRaVs infections.GLRaV-5 induces mitochondrial vesiculation**.**

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

1997 **Cabaleiro** *et al*.: GLRaV-3 is transmitted by *Planococcus citri* in a semipersisten 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 **Krastanova** *et al*.: GLRaV-2 and GLRaV-3 genes engineered in grapevine rootstocks to induce resistance.

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 specied 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.

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

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* (*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.

2000 **Zhou** *et al.*: New monoclonal antibodies to GLRaV-2, one of which is especially suited for ELISA testing.

2000 **Turturo** *et al*. : Partial sequencing of GLRaV-7 genome.

2000 **Sforza** *et al*.: New vectors of GLRaV-1 are the mealybugs *Heliococcus bohemicus* and *Phenacoccus aceris* and the soft scale insect *Pulvinaria vitis*.

2000 **Rowhani** *et al*.: Detection in California of a GLRaV-2 strain sharing about 74% sequence homology with GLRaV-2 type strain and reacting weakly serologically with GLRaV-2.

2000 **Seddas** *et al.*: Evidence that GLRaV-1 and GLRaV-3 are serologically related based on the cross-reactivity of a monoclonal antibody raised to GLRaV-1.

2001 **Little** *et al*.: Identification of hypervariable regions in GLRaV-1 genome. Evidence of the quasispecies nature of the virus.

2002 **Martelli** *et al.*: Revision of the family *Closteroviridae*. Establishment and description of *Ampelovirus* , a genus with monopartite RNA species, transmitted by mealybugs and soft scale insects. The type species is GLRaV-3

2002 **Alkowni** *et al.* : Report of a new putative grapevine leafroll associated virus.

2003 **Gugerli:** Updated review of leafroll and associated viruses.

2003 **Gòmez Talquenca** *et al.*: Learoll and GLRaV-1, GLRaV-2, and GLRaV-3 in Argentina.

2003 **Abou Ghanem -Sabanadzovic** *et al.*: Partial molecular characterization of Grapevine leafroll-associated virus 4.

2003 **Cornuet** *et al.*: Identification of a new putative ampelovirus (GLRaV-10?), later identified as a molecular variant of GLRaV-4.

2003 **Little and Rezaian**: Functional analysis of the genes of GLRaV-1. The presence of two ORFs conding for the coat protein duplicate is confirmed and the intracellular localization of some genome expression products is established. In particular, ORF 2-encoded protein induces the formation of endoplasmis reticulum vesicles which may be involved in virus replication.

2003 **Turturo** *et al.*: Genetic variability of GLRaV-3 studied by single-strand conformation polymorphism and nucleotide sequence analysis of fragments of three different genes. Evidence of the quasispecies nature of the virus.

2003 **Zhou** *et al*.: Production of monoclonal antibodies to GLRaV-3 elicited by linear epitopes located in the first portion of the coat protein gene.

2003 **Nölke** *et al.*: Generation of single chain antibody fragments to GLRaV-3 for induction of antibody-based resis tance in grapevine.

2004 **Alkowni** *et al.***:** Description and extensive sequencing of GLRaV-9, an ampelovirus first reported in 2002.

2004 **Ling** *et al*.: Nucleotide sequence of GLRaV-3 completed. The genome has a size of 17 919 nt and contains 13 genes.

2004 **Bertazzon** *et al.*: Molecular polymorphism of GLRaV-2 isolates studied by heteroduplex mobility assay identifies five clusters of molecular variants. The species quasi nature of the virus is confirmed.

2004 **Abou Ghanem-Sabanadzovic** *et al*.: Identification of a putative new closterovirus in cv Carnelian from California

2005 **Bertamini** *et al*.: GLRaV-3 infection reduces the amount of photosynthetis pigments, RuBP, nitrate reductase, photosynthetic activities, and thylakoid membrane proteins of field-grown cv. Lagrein vines, thus inducing a the rapid senesce of the leaves.

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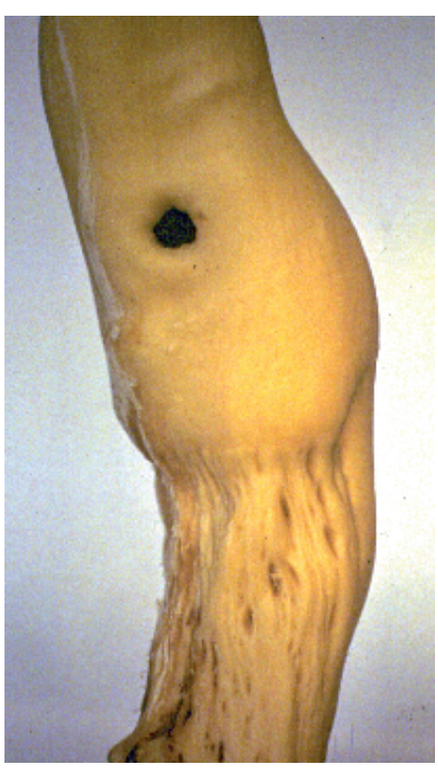
RUGOSE WOOD COMPLEX


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 usually latent in ungrafted *Vitis vinifera* and 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.); 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 roostocks, can show wood alterations. 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 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* or *Foveavirus*, family *Flexiviridae*, i.e. viruses with flexuous filamentous particles from about 730 to 800 x 12 nm, with distinct transverse cross banding. Vitiviruses and foveaviruses are phloem-restricted in grapevines, but whereas 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 x 10^6 that accounts for *c.* 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 associated agent of Grapevine rupestris stem pitting disease. 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. Viral RNA, which has been totally sequenced, has a Mol. wt of about 3.05 x 10^6 Da and a size of 8726 nt. The viral genome comprises 5 or 6 ORFs encoding, in the order, the replication-associated proteins (244 kDa), movement proteins (triple gene block, 25, 13 and 8 kDa) and the coat protein (28 kDa). The 6th ORF, when present, encodes a 14 kDa proteins with unknown function. 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 potexvirus.

Grapevine virus A (GVA), the type species of the genus *Vitivirus*, is the putative agent of Grapevine kober stem grooving. Virus particles are flexuous filaments about 800 nm long. Viral RNA has a Mol. wt of about 2.6 x 10^6 Da and a size of 7349 nt. 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), the coat protein (22 kDa) and a 10 kDa product which has nucleotide binding properties, is a pathogenicity factor and a gene silencing suppressor. Minor biological and serological variants of the virus are known.

Grapevine virus B (GVB) is a vitivirus distantly related serologically to GVA and one of the etiological 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 x 10^6 Da, a size of 7599 nt 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).

Grapevine virus C (GVC) is a little known and poorly characterized virus reported from Canada. Virus particles have a vitivirus morphology and an estimated length of about 725 nm. GVC is serologically distinct from GVA and GVB.

Grapevine virus D (GVD), a vitivirus distantly related serologically to GVA and GVB is associated with 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 c. 7600 nt and a 3' terminus structurally comparable to that of GVA and GBV.

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 all four vitiviruses (GVA, GVB, GVC, 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 were found to associate 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 vectors are the mealybugs *Planococcus citri, Pl. ficus, Pseudococcus longispinus, Ps. affinis, Heliococcus bohemicus,* and the scale insect *Neopulvinaria innumerabilis,* whereas GVB is transmitted by *Ps. longispinus, Ps. affinis,* and *Pl. ficus.* 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

were 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.

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 GRSPaV, the putative agent of rupestris stem pitting, with vein necrosis, as shown by 110R. Thus, it is plausible to regard 110R as a specific indicator of rupestris stem pitting in addition to *V. rupestris*. 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. In addition, other assays include: single step or nested reverse trascription-polymerase chain reaction (RT-PCR), immunocapture RT-PCR, or spot-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 make sanitary selection not 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. Control of mealybugs is difficult for they overwinter under the bark of grapevines and possess an unwettable waxy covering. Thus, no strategy has yet been developed for the chemical control of vectors. 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.

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**: First record of rugose wood in USA (California).

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 etiology.

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 (GSP-AV).

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 GSP-AV

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

1982 **Sarooshi** *et al*.: Rugose wood recorded from Australia.

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

1984 **Milne** *et al*.: Evidence that GSP-AV can occur in grapevines together with another similar but serologically unrelated virus with short closterovirus-like particles, denoted Grapevine virus B (GVB). GSP-AV 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 recorded from Brasil

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*.: First record of rugose wood from 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 *P.ficus*.

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

1990 **Engelbrecht and Kasdorf**: Natural field spread of corky bark in South Africa associated with the presence of *P. 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 x 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 GLRaV and corky bark. No closterovirus-like particles in samples with 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 Kd 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 recorded from Cyprus.

1991 **Boulila** *et al*.:Rugose wood recorded from Tunisia

1991 **Milkus** *et al.*: Rugose wood recorded from 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 recorded from 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 recorded from Spain

1993 **Boscia** *et al*.: Purification and properties of GVB. Virus transmission by the mealybug *Ps. 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 for the inclusion in the genus *Trichovirus.*

1994 **Merkuri** *et al.*: Rugose wood recorded from 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 recorded from Yemen.

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 recorded from 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 2002, 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 recorded from 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 recorded from Lebanon.

1996 **Tanne** *et al.*: A study of the spatial distribution pattern of corky bark in aThompson 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.*: GVA is transmitted by 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*.: Estasblishment of the genus *Vitivirus* with GVA as type species. GVA, GVB, GVC, 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 genome (GRSPaV).

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 a*l: 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 polyvynil difluoride membranes for virus detection in grapevine tissue extracts.

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 GRSPaV and Rupestris stem pitting.

2001 **Stewart and Nassuth:** An improved extraction method allows RT-PCR detection of GRSPaV virtually thoughout the year in all grapevine tissues. Samples made up of three buds from dormant canes are less laboriour to prepare than cane shavings and yield comparable results. Virus detected in bleached seeds suggesting that it is present inside the seeds.

2002 **Goszczynski and Jooste**: Use of single-strand conformation polymorphism reveals molecular heterogenity in GVA populations.

2002 **Dell'Orco** *et al*.: GVA particles carry a highly structured epitope centered on a common peptide region of the coat protein sequence.

2003 **Petrovic** *et al*.: GRSPaV particles, observed for the first time, are filamentous and measure 723 nm in length.

2003 **Dovas and Katis:** Improved RT-PCR method for the simultanous detection in grapevine extracts of vitivirus (GVA, GVB, GCD) and foveavirus (GRSPaV) sequences in two steps.

2003 **Galiakparov** *et al.*: The function of GVA genes identified by mutation analysis of individual ORFs of a full-length infectious viral clone.

2003 **Wang** *et al*.: Elimination of GVA by cryopreservation.

2003 **Habili** *et al.*: Rugose wood viruses in Iran.

2003 **Ahmed** *et al*.: Rugose wood viruses in Egypt.

2003 **Goszczynski and Jooste**: GVA and GLRaV-3 are both consistently associated with Shiraz disease in South Africa but only GVA seems to be required for disease induction.

2003 **Goszczynski and Jooste**: Thre groups of GVA strains (I, II, and III) identified in South Africa based primarily on sequence homology of the 3' end of the viral genome. Nucleotide sequence identity within groups is 91-99.8% and 78-89.3% among groups.

2003 **Kominek** *et al*.: Rugose wood viruses in the Czeck Republic.

2003 **Nakano** *et al*.: GVA transmission by *Pseudococcus comstocki.*

2003 **Meng** *et al*.: Western blots and ELISA using a polyclonal antiserum to recombinant coat protein of GRSPaV detect the virus in infected grapevine tissues almost with the same efficiecy of RT-PCR. The virus was not detected in 245 seedlings from infected cv. Seyval seedlings.

2003 **Minafra and Boscia**: Review of rugose wood-associated viruses.

2003 **Meng and Gonsalves**: Comprehensive review of the characteristics of GRSaV.

2004 **Adams** *et al.:* Establishment of the family *Flexiviridae*, comprising grapevine viruses belonging in the genera *Vitivirus, Trichovirus* and *Foveavirus.*

2004 **Zorloni** *et al*.: Experimental transmission of GVA by the mealybug *Heliococcus bohemicus.*

2004 **Bouyahia** *et al*.: An association exceeding 95% observed between GRSPaV and 110R vines showing vein necrosis symptoms in indexing trials. No veing necrosis observed in 110R top grafted on GRSPaV-free *V. rupestris*. Suggestion than vein necrosis is a specificic reaction of 110R to GRSPaV.

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GRAFT INCOMPATIBILITY

GRAFT INCOMPATIBILITY

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/rooststock 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). 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 France, Argentina and probably elsewhere. 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, although none of a number of known grapevine-infecting viruses has been found in affected vines, except for GRSPaV. 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 Argentinian 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.

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 clonal selections 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 sauvingon 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.

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FLECK COMPLEX

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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 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 (c. 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 Mr of c. 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 x 10^6) is 7564 nt in size and contains four open reading frames (ORF) that

encode a 215.4 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 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:

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 in 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 is of no epidemiological importance. 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.

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 unrealiable. 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 survey.

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.

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 Brazil, based on the differential reactions of indicators

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 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*.

2001 **Sabanadzovic** *et al*.: Complete nucleotide sequence of 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.

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MINOR 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. 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. Grapevine berry inner necrosis).

A. European diseases

GRAPEVINE YELLOW MOTTLE

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. Yellow mottle has been reported from Germany, Switzerland, Hungary, former Czechoslovakia, Bulgaria, and Turkey.

Agent: *Alfalfa mosaic virus* (AMV), the type species of the genus *Alfamovirus,* is the putative causal agent. 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 c. 18% of the particle weight, with the following mol. wts: RNA-1, 1.04 x 10^6 Da (3644 nt); RNA-2, 0.73 x 10^6 (2593 nt); RNA-3, 0.62 x 10^6 (2037 nt). Capsid proteins subunits are of one type, with Mr 24x 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.

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 x 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 37 days at 37-38°C.

1978 **Jankulova**: AMV infections recorded from Bulgaria.

1981 **Beczner and Lehoczky**: AMV infections recorded from Hungary. Chardonnay and Veltliner rouge précoce identified as reliable indicators.

1985 **Francki:** Comprehensive review of the properties of AMV and 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 infections recorded from Turkey**.**

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Akbas B. and G. Erdiller, 1993. Researches on grapevine virus diseases and determination of their incidence in Ankara Turkiye. *Journal of Turkish Phytopathology* **22**, 55-63.

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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. This disease is known to occur only in Hungary.

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.

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.

3. References

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RODITIS LEAF DISCOLORATION

1. Description

Main synonyms: None.

Main symptoms: Symptoms are prominent in late summer and consist of yellow and/or reddish discolourations 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 discoloured sectors. Bunches are reduced in numbers, size and have low sugar content. The disease has been recorded only from Greece.

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 *c.* 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 with diseased grapevines.

Transmission: No vector is known. The disease is graft-transmissible and spreads through infected propagating material.

Varietal susceptibility: No information.

Detection: Graft-transmission to *V. vinifera* cv. Mission. Viruses associated with the disease are readily transmitted by sap inoculation and can be detected by ELISA and molecular techniques.

Control: No information.

2. Historical review

1989 **Rumbos and Avgelis**: Roditis leaf discoloration described in Greece. Evidence of its graft-transmissibility.

1991 **Avgelis and Rumbos**: Double infection of diseased vines by GFLV and CarMV reported.

3. References

Avgelis A.D. and I.C. Rumbos, 1991. Carnation mottle virus isolated from vines affected with "Roditis leaf discoloration". *Proceedings 10th Meeting of ICVG, Volos 1990*, 437-443.

Rumbos I.C. and A.D. Avgelis, 1989. Roditis leaf discoloration -- a new virus disease of grapevine: symptomatology and transmission to indicator plants. *Journal of Phytopathology* **125**, 274-278.

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. The disease has been recorded only from Greece.

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 *Tobacco streak virus* (TSV), but differs from GLPV, the only other ilarvirus reported from grapevine.

Transmission: GAMV is pollen-borne in herbaceous hosts and was able to infect pollinated plants. Whether this mechanism operates with grapevines has not been ascertained. Infected grafting material is likely to be responsible for virus dissemination.

Varietal susceptibility: No information

Detection: Indexing on cv. Baresana x Baresana, mechanical transmision to herbaceous hosts, and ELISA.

Control: No information

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.

3. References

Girgis S.M., F. P. Bem, P.E. Kyriakopoulou, C.I. Dovas, A.P. Sklavounos, A. Avgelis, N. Katis, S. Tzortzakakis and M. Tsagris, 2000. A new ilarvirus isolated from grapevine in Greece. *Plant Disease* **84**, 1345.

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YELLOW LINE PATTERN *(Rasperry bushy dwarf virus)*

1. Description

Main synonyms: None

Main symptoms: Grapevines 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 (Mr *c*. 30 x 10^3), a dimeter of about 33 nm, and a bipartite single-stranded RNA genome accounting for *c*. 24% of the particle weight and consisting of two functional species RNA-1 with Mol. wt of 2 x 10^6 Da (5.5 Kb in size) and RNA-2 with Mol. wt 0.8 x 10^6 Da (2.2 kb in size).

Transmission: In raspberry the virus infects progeny seedlings and pollinated plants through pollen. The vay of natural spreading in grapevine, if any, is unknow. However, infected propagative material can disseminate the RBDV.

Varietal susceptibility: No information

Detection: Mechanical transmission to herbaceous hosts, ELISA , and RT-PCR.

Control : No information

2. Historical review

1976 **Murant**: Description of RBDV**.**

2003 **Mavric** *et al*.: First record of RBDV in grapevine.

3. References

Mavric I., M. Virscek Marn and I. Zezlina, 2003. Raspberry bushy dwarf virus infection of grapevine in Slovenia. *Extended Abstracts 14th Meeting of IGVG, Locorotondo 2003,* 20

Murant A. F., 1976. Raspberry bushy dwarf virus. *CMI/AAB Description of Plant Viruses,* No. 165

B. Japanese diseases

GRAPEVINE BERRY INNER NECROSIS

1. Description

Main synonyms: None

Main symptoms: Infected grapevines have low vigor, delayed bud break and young shoots with short internodes and internal browning. Chlorotic mottling, rings and line patterns are shown by leaf blades. Ripening of bunches is delayed, berries are small and show external discolorations and internal necrosis. Grapevine berry inner necrosis has been reported only from Japan, representing the most important virus disease in Yamanashi Prefecture.

Agent: The 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 7.5 x 10^6 Da, the 3' terminal region of which (2469 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.

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*

3. References

Kunugi Y., S. Asari, Y. Terai and A. Shinkai 2000. Studies on the grapevine berry innner necrosis virus disease. 2. Transmission of grapevine berry inner necrosis virus by the grape erineum mite *Colomerus vitis* in Yamanashi. *Bulletin of Yamanashi Fruit Tree Experimental Station* **10**, 57-63.

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Tanaka H., 1984. Mosaic symptoms on cv Kyoho. *Annals of the Phytopathological Society of Japan* **55**, 536

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Terai, Y., Kunigi Y. and Yanase H., 1993. A new virus disease, grapevine berry inner necrosis with natural spread in Japan. *Extended Abstracts 11th Meeting of ICVG, Montreux 1993*, 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.

Yanase H. and 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., H. Iida, S. Goto, H. Magome, T. Takahashi and Y. Terai, 1997. Grapevine berry inner necrosis, a new trichovirus: comparative studies with several known trichoviruses. *Archives of Virology* **142**, 1351-1363

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. The disease has only been reported from Japan.

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.

Detection: Grafting to 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., T. Iwanami, S. Yamashita, Y. Doi and M. Hatamoto, 1986. Three phloem-limited viruses of grapevine: direct fluorescence detection. *In* Plant Virus Diseases of Horticultural 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. The disease has only been reported from Japan.

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.

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., S. Yamashita, Y. Doi and K. Yora, 1979. A small spherical virus associated with the ajinashika disease of Koshu grapevine. *Annals of the Phytopathological Society of Japan* **45**, 70-73.

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Namba S., D. Boscia, S. Yamashita, T. Tsuchizaki, and D. Gonsalves, 1991. Purification and properties of spherical virus particles associated with grapevine ajinashika disease. *Plant Disease* **75**, 1249-1253.

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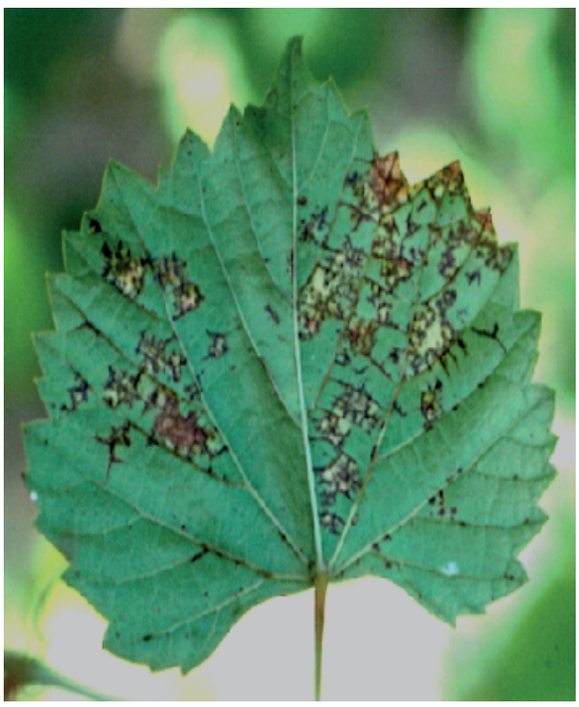

VIRUS-LIKE DISEASES

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 run more or less parallel to the main veins. Basal leaves, whether they bear enations or not, are often mis-shapen, 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 mis-shapen, and often show longitudinal cracks between the nodes. Leaves developed later in the season are usually normal. The crop can be 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 etiology of enation disease is not yet clear. Graft transmission suggests that it is a virus disease, and the frequent occurrence of fanleaf virus in enation bearing vines supported the hypothesis that enation disease could be due to a severe strain of fanleaf virus. This hypothesis, however, has now been dismissed

Transmission: By vegetative propagation. The transmission by graft is rather erratic. The infectious agent of the disease perennates in propagating material.

Varietal susceptibility and sensitivity: There is little information available. Symptoms have been observed on many *V. vinifera* varieties in Europe, North America (California), North (Tunisia) and South Africa, Latin America (Venezuela), Australia and New Zealand. The varieties Panse Precoce, Primus, Italia, Riesling, Grenache and Tokay appear to be quite susceptible and develop severe symptoms when infected.

Detection: By observing the symptoms on the leaves and by indexing on LN 33 hybrid. However, as symptom expression is variable in successive years and graft transmission not 100 % successful, the absence of symptoms does not necessarily mean that the plant is healthy.

Control: Use of healthy material. There is no information on the possibility of curing this disease by heat treatment or meristem culture.

2. Historical review

1891 **Buchenau**: First description of enation disease of grapevine occurring in Germany, with drawings of symptoms.

1937 **Gigante** : Research on histological and cytological aspects of enations.

1954 **Hewitt**: Description of 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 gave no results.

1966 **Graniti** *et al*.: Detailed description of macroscopic and microscopic symptoms of enation disease, historical account, attempts to transmit the disease by graft, with negative results. There is some evidence that enation can be carried in the rootstocks. Mechanical transmission tests were also negative, only fanleaf virus was recovered. The authors conclude that the disease is probably of European origin, and possibly caused by a virus. The possible role of fanleaf virus in the etiology of enation requires further investigation.

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 fanleaf virus, but report on observations made in Australia where no fanleaf virus could be 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%), 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*.: In experiments on graft transmission of enation disease aimed at determining the best indicator, the hybrid LN 33 was found to be the most sensitive and reliable indicator variety, although the rate of symptom expression 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 severità of symptom expression.

1997 **Padilla** *et al*. ; Enation disease in Spain

1997 **Chabbouh and Savino**: Enation disease in Tunisia

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VEIN MOSAIC

1. Description

The symptoms of vein mosaic have been confused for some time with those of fanleaf/yellow mosaic, but when fanleaf virus transmission to herbaceous hosts became possible, it was clear that vein mosaic was not caused by fanleaf virus. This disease is widespread and probably worldwide. A similar disease has been reported in Australia under the name of summer mottle. Vein mosaic appears to be of low economic importance.

Main synonyms: Mosaïque des nervures (Fr.), Adernmosaik (Germ.), Mosaico delle nervature (Ital.).

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 varieties, areas of the leaf blade may become necrotic, but these necroses do not affect the veins as it is the case with 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 graft and vegetative propagation. No vector known.

Varietal susceptibility and sensitivity: *Vitis riparia* Gloire de Montpellier is especially sensitive and is used as indicator. LN 33 is also sensitive. Several *V. vinifera* cvs. show symptoms (Syrah, Servant, Viognier, Chardonnay, Alphonse Lavallée, Muscat de Hambourg, Pearl of Csaba). Chasselas, Pinot, and Gamay apparently show little or no symptoms.

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 (unpublished).

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Kuniyuki H., 1985. Adverse effect of light and of high temperature on symptom expression of grapevine vein mosaic in Sao Paulo. *Summa Phytopathologica* **11**, 48-49
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Saric A. and Hranuelli T., 1977. Investiation on grapevine viruses in the SR Croatia. *Proceedings of the Conference on Excoriosis and Virus Diseases of Grapevine, Mostar 1977*, 149-141.
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Vuittenez A. and G. Stocky, 1982. Ultrstructure de vignes infecteés par deux maladies de type viral: la mosaique des nervures, ou la “feuille rouge”. *Proceedings 7th Meeting of IGCV, Niagara Falls 1980*, 191-204.
Woodham R.C. and L.R. Krake, 1983. A comparison of grapevine summer mottle and vein mosaic diseases. *Vitis* **22**, 247-252.

SUMMER MOTTLE

Summer mottle, an Australian disease, resembles in some respects the European vein mosaic and the Greek Roditis leaf discolouration (see under Minor virus diseases). 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 was immune to infection. *V. rupestris* and LN33 are infected symptomlessly. However, several European grape cultivars show symptoms.

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

3. References

Barlass M., K.G.M. Skene, R.C. Woodham and L.R. Krake, 1982. Regeneration of virus-free grapevines using *in vitro* apical culture. *Annals of Applied Biology* **101**, 291-295.

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VEIN NECROSIS

Although vein necrosis is currently regarded as a disease in its own right, recently an association exceeding 95% has been experimentally observed between *Grapevine rupestris stem pitting-associated virus* (GRSPaV) and vines of *V. rupestris* x *V. berlandieri* 110 Richter (110R) with vein necrosis symptoms. This strongly supports the hypothesis that vein necrosis is a specificic reaction of the rootstock 110 R to GRSPaV infection.

1. Description

Vein necrosis has probably a worldwide distribution. So far, its economic importance has not been assessed, and the only *Vitis* species that is clearly affected is the rootstock 110 R.

Main synonyms: Nécrose des nervures (Fr.), Adernnekrose (Germ.), necrosi delle nervature (Ital.).

Main symptoms: On the rootstock 110 R., 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 on the lower face of the leaf blade. Also the tendrils and many shoots can necrotize, especially under greenhouse conditions, and some infected plants may die.

Agent: Suspected to be a virus, most likely GRSPaV. Mycoplasma-like organisms have been observed in the phloem of symptomatic vines, but their etiological relationship with the disease has not been proven.

Transmission: By grafting and vegetative propagation. No vector known.

Varietal susceptibility and sensitivity: The rootstock 110 R is most sensitive. Little is known about sensitivity of other *Vitis* species, varieties or hybrids. Many grapevine varieties and rootstocks are infected symptomlessly.

Detection: By grafting on 110 R. 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 110 R 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 this virus-like disease 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 R.C. and L R. 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 is on the average 71 %. Heat therapy reduced this proportion to 35.5 %, 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 Greese

1992 **Martelli** *et al*.: Vein necrosis in Malta

1993 **Golino**: Vein necrosis in California

1994 **Khun:** Vein necrosis in Brazil

2004 **Bouyahia** *et al*.: An association exceeding 95% observed between GRSPaV and 110R vines showing vein necrosis symptoms in indexing trials. No veing necrosis observed in 110R top grafted on GRSPaV-free *V. rupestris*. Suggestion than vein necrosis is a specificic reaction of 110R to GRAPaV.

3. References

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Rumbos I C., 1989. Vein necrosis, fleck and leafroll in *Vitis vinifera* and grapevine rootstocks in central Greece. *Phytoparasitica* **17**, 61

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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 nucleotides, 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.

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Hadidi A., R. Flores, J.W. Randles and J.S. Semancik (eds.), 2003. Viroids. CSIRO Publishing, Collingwood, 370 pp.

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, however, 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 both belong in the genus *Apscaviroid.* Both these viroids wer first isolated in Australia, respectively from a cv. Cabernet franc and a cv. Kyoto vine 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

The three additional viroids that have been detected in grapevines, HSVd-g, CEVd-g, and AGVd, are not associated to any specific symptomatology.

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, the USA, and Tunisia.

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 gardens 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 so far has only been recorded from Australia and the USA, besides Spain.

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.

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 (hybridization and RT-PCR) which constitute far better detection and identification tools.

Control: Use of viroid-free propagative material obtained by meristem tip culture.

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 etiology 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** *et 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)
Australian grapevine viroid (AGVd).

1996 **Wang** *et al*.: First record of grapevine viroids in China.

1997 **Flores** *et al.:* Review of viroids.

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.

2003 **Little and Rezaian**: Updated review of grapevine viroids.

2003 **Elleuch** *et al*.: First report of AGVd in the Mediterranean.

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YELLOWS

GRAPEVINE YELLOWS: GENERAL PROPERTIES

1. Description

Grapevine yellows (GYs) are a group of severe phytoplasma-induced diseases occurring worldwide on a number of *Vitis vinifera* cultivars. The different GYs cannot be differentiated on the basis of symptoms. The first GY to be recorded was Flavescence dorée in France in the 1950's. However, it was mainly in the 1990's that GYs could be differentiated, after their aetiology had been understood and molecular methods for the characterization of associated phytoplasmas had been developed. The main characteristics of GY diseases are important losses or damage to the yield, a severe decline of the vine, persistence of infection in dormant plant material, and transmission by specific leafhopper or planthopper vectors. The occurrence and spread of a particular GY mainly depend on the presence of efficient vectors in the vineyards or their close vicinity. However, vector species have not been identified for all GY diseases.

Main synonyms: Flavescence dorée-like disease, Vergilbungskrankheit, Golden flavescence, Flavescenza dorata, Amarilliamento.

Main diseases: Flavescence dorée, Flavescenza dorata, Bois noir, Vergilbungskrankheit, Schwarzholzkrankheit, Legno nero, Palatinate grapevine yellows, Australian grapevine yellows, North American grapevine yellows.

Main symptoms: Young shoots of affected *Vitis vinifera* are weak with short internodes and frequent necrosis of terminal buds. Downwards rolling of the leaves and sectorial discolorations of the blades, involving also the main veins, develop on leaves. Red-berried varieties show reddish to purple discolorations while white-berried varieties show golden to chlorotic discolorations. Leaf blades are crispy and brittle. Bunches wither in early summer or berries shrivel later in season, resulting in reduction of quantity and quality of the crop. Characteristic symptoms in the end of summer are a partial or total lack of lignification which may affect individual canes and shoots or the whole plant, depending on the particular disease and other conditions such as variety, climate and infection pressure. Rubbery canes fall downwards with a typical "weeping" aspect. Quite often, autumn fall of leaves occurs later on diseased than on healthy vines. Severely infected stocks decline rapidly.

Agents: Phytoplasmas were called Mycoplasma-like organisms (MLOs) from their discovery in 1967 until the International Committee of Systematic Bacteriology (ICSB) replaced this name with the term phytoplasma in 1993. They are wall-less, phloem-restricted bacteria that belong to the class Mollicutes.

Phytoplasma cells are vesicular rounded bodies, variable in shape and size (50-1000 nm in diameter) that circulate in phloem sieve tubes and can be seen in the electron microscope passing through pores of sieve plates. However, their movement is slow and their distribution in the plant is erratic. Their titre is usually very low in grapevine, though some sieve tubes may appear crowded with phytoplasma cells in the electron microscope. Nevertheless, all organs of the plant may be infected, including roots, canes, shoots, buds, inflorescence and berries, but not seeds.

Phytoplasmas have the smallest genome reported for procaryotic organisms (560 2,200 kbp). Nonetheless, their genome is poorly known because they cannot be cultivated. Phytoplasmas form a homogeneous phylogenetic clade subdivided into about 20 groups and subgroups, based mainly on sequence similarity of their rRNA genes and of a few other genes, such as the ribosomal protein genes or the elongation factor Tu, in addition to other criteria such as symptomatology, host range, and serology. In 1997, the term phytoplasma has become the genus name of these plant pathogenic agents under the provisional taxonomic status *Candidatus*. Several *Candidatus* phytoplasma species have been recently described.

GY agents have been identified in no less than 5 groups of phytoplasma clade. Flavescence dorée (FD) and Palatinate Grapevine Yellows (PGY) phytoplasmas belong to group 16SrV (or Elm yellows group). Stolbur phytoplasmas, associated to Bois noir (BN), Vergilbungskrankheit (=Schwarzholzkrankheit) or Legno nero and also one of the agents of Australian grapevine yellows (*Candidatus* Phytoplasma australiense) belong to group 16SrXII (or stolbur group). Phytoplasmas in the 16SrIII group (or X-disease group) are associated with grapevine yellows in North America and Israel. *Candidatus* Phytoplasma australasia, a phytoplasma belonging to group 16SrII (or peanut witches'

broom group) is a second agent of Australian grapevine yellows. Phytoplasmas in the 16SrI group (or aster yellows group) are associated with endemic GY diseases in several countries of Europe and in the USA. Double infections have been reported.

Transmission: Phytoplasmas are vectored by hemipters, mainly hoppers (cicadellids or cixiids) or psyllids. The three ascertained vectors of GY diseases are univoltine leafhopper or planthopper species. Phytoplasmas persist in their vectors but vertical transmission to the progeny of infected gravid females is not possible or scarce.

Phytoplasmas also persist in vine stocks during winter. Propagation material may be the infection source for long distance dissemination of GY diseases. Though the rate of transmission to plant material can be very low, such type of transport is risky when potential insect vector species occur on the site of planting.

Varietal susceptibility and sensitivity: Numerous *V. vinifera* cultivars have been reported to be sensitive or very sensitive to GYs in all countries where infection occurs. It is probable that the feeding preference of insect vectors, as well as their feeding activity, influence symptom expression and differential sensitivity of cultivars. Some cultivars such as Chardonnay, Pinot noir, Cabernet Sauvignon, Riesling and also numerous local varieties, are very sensitive to all GY diseases. The situation of cv Syrah is controversial. Full recovery and transient remission of symptoms have been observed in low and medium sensitive cultivars, which allows restoring the sanitary status of affected vineyards when the vector activity is controlled. These phenomena also depend on the disease complex (phytoplasma, vector and abundance of reservoirs).

Vitis riparia and American rootstock varieties and hybrids do not show typical symptoms of GY. Infection of rootstocks has been detected only in the case of Flavescence dorée but it cannot be excluded for other GY agents.

Other host plants: Most phytoplasmas are ubiquitous plant parasites that can be hosted by several sometimes tolerant plant species. Hence, numerous plants or weeds may be overt or discrete reservoirs from which acquisition of phytoplasma by vectors is possible according to the feeding preference of each species. However, when grapevine is not a preferred host for the vector, erratic transmission to grapevine may nevertheless take place.

Detection: GY syndrome is characteristic. Simultaneous presence of symptoms on leaves, shoots, canes, and bunches is strong evidence for phytoplasma infection. Individual symptoms can be confused with other diseases or disorders.

Phytoplasmas can be detected by graft transmission to sensitive vines. They can also be observed in sieve tubes by light microscopy, using DAPI staining, but the latter technique has never been successfull on field-grown grapevines. Detection can also be made by transmission electron microscopy of thin sections or by scanning electron microscopy. These methods are not specific for any phytoplasma and are too laborious for disease monitoring.

Polyclonal and monoclonal antisera have been raised to a few phytoplasmas, including the agents of FD and BN. ELISA detection is possible from vascular tissue of symptomatic grapevines. The best antigen source are leaf veins and petioles. Particular procedures for extraction of phytoplasma antigens from infected vines must be used to enhance the sensitivity of detection.

Outstanding progress in detection was achieved with DNA-based techniques. A range of primers that can be used for amplification with Polymerase Chain Reaction (PCR) of characteristic DNA fragments of phytoplasmas, are available in the literature. Most of these PCR primers have been designed on conserved regions of the rRNA gene and are "universal" for all known phytoplasmas. Others, designed on variable regions of the rDNA, on less conserved genes, or on random selected non-ribosomal DNA fragments, are group specific. The extraction from infected tissues of total DNA containing enough phytoplasma DNA of good quality and the elimination of inhibitors of the PCR reaction, are critical.

When no information on the particular phytoplasma type is available, PCR amplification with universal primers is preferred. Then, Random Fragment Length Polymorphism (RFLP) analysis of the amplicon can provide further characterization of the infecting phytoplasma. When the presence of a particular disease is suspected, more specific primers can be used.

Other molecular methods are being developed, using detection of PCR amplification products with DNA-DNA hybridization with a specific probe. Real-time PCR has also been successfully used.

Detection of phytoplasma DNA can be achieved from all plant organs or insect vectors. Generally, phytoplasmas are unevenly distributed in GY-affected vines. Detection in the upper parts of the vines is usually done from veins and petioles of the leaves of symptomatic shoots, but is also possible using young leaves shortly before symptom expression or phloem scrapings from lignified canes. Non-symptomatic grapevines that show irregular symptoms from one year to the next may also test positive. FD can be detected from leaves of non-symptomatic American roostocks.

However, even sensitive detection methods may not be fit for use in sanitary selection because of the uneven distribution of phytoplasmas in mother plants and their vegetative progeny.

Control: There are no direct curing methods of infected plants. Pruning or top-grafting are useless because roots and trunks are infected. Control of GY diseases depends on the knowledge of vector insect species, on the possibility to limit or eradicate their population and prevent their migration or movement in vineyards, and on the identification of reservoirs of inoculum such as infected grapevines, weeds or other crops.

In any case, efforts should address prevention by planting healthy propagation material and limitation of vector populations and their inoculative activity.

Production of sanitized propagation material is possible with hot water treatment (HWT), i.e., soaking of dormant material before or after grafting, into hot water (50 °C) for a sufficient length of time (minimum 30 mn).

Control methods of vector populations are being experimented with natural insecticides, cultural practices, and natural enemies.

Investigations are being conducted on sensitivity, tolerance and potential for recovery of varieties, on physiological changes and defence mechanisms induced by infection, and on elicitors of defence reactions to these phloem-restricted bacterial agents.

2. Historical review

1955 **Levadoux**: Description of a severe outbreak of "Flavescence dorée" on Baco 22A in southwestern France. The author suggests this disease to be due to adverse climatic and soil conditions, but does not rule out the possible involvement of a pathogen.

1956 **Branas** (a and b): Description of flavescence epidemics on Baco 22A and Chardonnay in France. The disease is thought to be caused by root damage.

1957 **Caudwell**: Characterization of a new type of flavescence, denoted Flavescence dorée (FD) in agreement with the name proposed by Levadoux (1955) because of the golden yellow metallic aspect of leaves. Symptoms (macroscopic and microscopic), evolution of the disease in space and time, hypotheses on its nature. The disease can be transmitted by grafting and is probably a virus disease.

1961 **Caudwell** (a): Studies on Bois noir (BN) and on its relationships with FD. BN is considered as a non epidemic form of FD.

1961 **Caudwell** (b): Description of recovery in grapevines affected with FD.

1961 **Schvester** *et al*. FD is transmitted by the leafhopper *S. littoralis* Ball, an insect that has been introduced recently from America.

1964 **Vidano**: *S. littoralis* Ball found in Italy in 1963. The biology of the insect is described.

1965 **Gärtel**: Description, under the name Flavescence dorée, of a disease occurring in the vineyards of the Mosel Valley and of the Rhine Valley.

1966 **Caudwell**: Attempts to inhibit the agent of FD *in vivo* by heat treatment. Immersing cuttings taken on FD-affected grapevines in water at 30°C prior to planting reduced the proportion of infected plants by about 83%.

1967 **Doi** *et al*.: Discovery of Mycoplasma or PLT group-like microorganisms in the phloem elements of plants showing dwarfing, witches' broom and yellowing.

1968 **Baggiolini**: *S. littoralis* Ball is present in Ticino (southern Switzerland).

1970 **Rafaila and Costache**: Yellows of grapevine with symptoms similar to those of FD found in 1967 for the first time in Romania, mainly on cv. Regina.

1971 **Caudwell** *et al.* (a): Mycoplasma-like organisms (MLOs) are observed in diseased grapevines and infective leafhoppers and in *Vicia faba* submitted to feeding inoculation with infective *S. littoralis*.

1971 **Caudwell** *et al*. (b): Evidence that FD and BN are two different diseases with similar symptoms. Potential existence of several different diseases: leafhoppers (*Euscelidius* sp. and *Euscelis* sp.) caught in the vicinity of vineyards could transmit a yellows disease to *Vicia faba* plants. Symptoms on *V. faba* are different from those obtained with feeding inoculation with infective *S. littoralis*. Inoculation of grapevine seedlings with *S. titanus* fed on the latter *V. faba* plants produced typical GY symptoms. This phytoplasma was later on identified as a Clover phyllody phytoplasma.

1973 **Belli** *et al*.: Presence of a disease similar to FD in the Oltrepò Pavese (northern Italy). The disease has been observed for the first time in 1968.

1973 **Tanne and Nitzany**: Occurrence of a yellows disease resembling FD in Israel.

1975 **Osler** *et al*.: *S. littoralis* is present in the same region of Oltrepò Pavese.

1977 **Rumbos** *et al*.: Rickettsia-like organisms observed in roots of grapevines with "Vergilbungskrankheit" in the Saar, Mosel and Rhine regions are considered as the causal pathogens of this disease. As similar organisms have been found in nematodes of the species *Xiphinema index*, the hypothesis is put forward that this nematode is the vector of the disease. So far, these findings have not been confirmed.

1979 **Caudwell and Larrue**: Spread of FD in France is related to sanitary status of planting material. Recommendation that mother plants should be grown in areas far away from FD-infected regions.

1980 **Caudwell**: Symptoms of grapevine yellows (Amarilliamento) reported in Chile on cv Elqui.

1982 **Caudwell** *et al*.: Production of antisera to FD-MLO raised to extracts of experimentally FD-infected plants (*Vicia faba*) and leafhoppers (*Euscelidius variegatus*) and first microscope observation of MLOs trapped with ISEM.

1982 **Magarey and Wachtel**: Description of a new disease of grapevine of the yellows type on the cv Rhine Riesling in South Australia. Provisory name "Rhine riesling problem". First record in 1975-76.

1983 **Caudwell**: Discussion on the origins of yellows diseases of plants, with special reference to grapevine. The author assumes that both FD and its vector were introduced from North America with varieties of *Vitis labrusca* between 1927 and 1950. Conversely, Bois noir, of which *S. titanus* (= *littoralis*) is not a vector, is probably of European origin.

1984 **Credi and Babini**: Grapevine yellows are reported in Emilia Romagna (Italy).

1985 **Belli** *et al.*: *S. titanus* found in 1984 in vineyards of northern Italy. An important FD-like disease is reported.

1985 **Granata**: Description of an epidemic yellows disease on cv Inzolia in Sicily.

1985 **Rumbos and Avgelis**: Observations of a FD-like disease in Greece with severe symptoms on cvs Razaki and Roditis.

1986 **Boudon-Padieu and Larrue**: ELISA detection of FD pathogen on infected reared experimental and wild natural leafhopper vectors (*E. variegatus* and *S. titanus,* respectively).

1986 **Carraro** *et al*.: Presence and distribution of a FD-like disease in the region Friuli-Venezia Giulia in Italy.

1986 **Conti**: A review of intracellular procaryotic phytopathogenic agents.

1986 **Martelli**: A review on the knowledge on grapevine diseases induced by phloem- or xylem-limited prokaryotes in Europe.

1986 **Mescalchin** *et al*.: Occurrence of FD-like symptoms in the valley of Sarca in Trentino, northern Italy.

1987 **Borgo** *et al*.: Description in Italy of the presence of FD or FD-like diseases, that are responsible for severe decline of vines. However, their etiology is unclear.

1987 **Credi** *et al*.: Presence of a FD-like disease in Emilia-Romagna, Italy.

1987 **Fortusini and Belli**: Description of the development of epidemics of FD-like diseases in northern Itay. Susceptibility and sensitivity of affected varieties (Chardonnay, Pinot bianco, Pinot nero) and comparison with other similar diseases.

1987 **Rui** *et al*.: Contribution to the knowledge of FD (or similar diseases) in the Veneto region, Italy. Chardonnay is the more affected variety. Survey for the presence of *S. titanus*, vector of FD, disease distribution, control measures.

1987 **Seljak**: Presence of *Scaphoideus titanus* in western Slovenia (Yugoslavia).

1987 **Vidano** *et al*.: Study on the distribution of *S. titanus*, vector of FD, in viticultural areas of northern Italy and of other Auchenorrhynchas susceptible to play a role in the transmission of yellows diseases in this region.

1988 **Credi and Callegari**: Survey of vineyards in Emilia-Romagna, Italy, for the presence of a FD-like disease. The results suggest that the disease is brought into the vineyards from outside local sources.

1988 **Egger and Grasselli**: Presence in Toscana, Italy, of a FD-like disease on Chardonnay.

1988 **Fortusini** *et al*.: New data on the spread of FD in three vineyards of Oltrepò pavese (northern Italy) from 1985 to 1987. Two of these vineyards were sprayed with insecticides in 1986 and 1987, resulting in a reduced diffusion of the disease, whereas an unsprayed vineyard was more affected.

1988 **Magarey** *et al*.: Observation of MLOs in phloem tissue of yellows-affected grapevines in Australia.

1988 **Quaroni** *et al*.: Observations, using the scanning electron microscope, of MLOs in phloem tissues of grapevines affected by "FD" in northern Italy.

1988 **Vidano** *et al*.: Survey of potential Auchenorryncha vectors of the pathogen agent of FD in Piemonte (Italy). In addition to *S. titanus*, *Hyalesthes obsoletus, Euscelidius variegatus* and *Euscelis incisus* are taken into consideration.

1989 **Borgo**: General information on the presence of FD-type diseases in northern Italy. *S. titanus* is not always associated to the disease.

1989 **Credi**: Description of a FD-like disease in Emilia Romagna and the reaction of 3 different cultivars. Recovery and crop loss are variable.

1989 **Rumbos**: Review of the knowledge on the etiology of grapevine yellows and observations with the scanning electron microscope of root and petiole tissues from diseased and unaffected plants of cv Riesling. The aetiology is not fully ascertained though the presence of MLO is probable.

1989 **Vidano** *et al*. (a and b): Identification of numerous species of Auchenorrhynchas in the vineyard ecosystem in Piemonte (northen Italy) and of ampelophilous species. Several weeds with symptoms of phyllody were found to contain MLO in electron microscope studies. Natural infection with MLOs of bait plants (*Catharanthus roseus* and *Vicia faba*) placed in vineyards in spring and summer. The authors recommend that research continues on techniques for the ecological control of weeds and of leafhoppers linked to them and on the aetiology of the different forms of "golden flavescence".

1990 **Caudwell**: Review on the epidemiology and characterization of FD and other GY diseases.

1990 **Caudwell** *et al*.: Grapevine graftwood shoots infected with FD can be disinfected by hot water treatment in the dormant stage. The recommended temperature / time combination is 50°C / 35-60 min. Treatment prior to storage is more efficient.

1990 **Credi** *et al*.: Bench grafting experiments of buds of indicator cvs. Chardonnay and Baco 22A grafted on donor yellows-diseased plants of cvs Pinot blanc and Sangiovese. Only part of the plants were infected. Symptoms also developed on plants obtained from buds taken on diseased Chardonnay and Sangiovese grafted on healthy Kober 5BB.

1990 **Granata and Russo**: An epidemic disease with FD-type symptoms develops in Sicily on cv. Inzolia.

1991 **Conti**: A yellows-type disease of cv. Chardonnay develops in Tuscany. *S. titanus* was not found in the area. Similar symptoms on Chardonnay could be obtained by insect inoculation (*Euscelis incisus*) and by cleft-grafting of tissues taken from yellows-infected elm.

1991 **Credi and Santucci**: Development of "Flavescenza dorata" in grapevine in Emilia-Romagna and rate of infestation in different systems of cultivation. The annual rate of symptomatic plants was never greater than 20 % over a 6-year period.

1991 **Deng and Hiruki**: A method to amplify 16S rRNA gene from culturable and nonculturable mollicutes. Specific primers can be used for MLOs. This is a prospect for investigation on MLOs associated to plant yellows.

1991 **Di Terlizzi** *et al*.: Presence of yellows-like symptoms in Apulian grapevines (central Italy).

1991 **Granata and Grimaldi**: MLOs are observed with the electron microscope on affected grapevines of cv. Inzolia in Sicily.

1991 **Marinesku** *et al*.: Occurrence of grapevine yellows in Moldavian SSR.

1991 **Refatti** *et al*.: The FD-like disease developing in Friuli-Venezia Giulia since the early 1980's was not decreased significantly in vineyards sprayed with insecticides though *S. titanus* was present in all vineyards checked.

1992 **Ahrens and Seemüller**: Oligonucleotides selected in the conserved parts of the 16S rRNA gene of MLOs can be used with polymerase chain reaction (PCR) to amplify a sequence of the gene in several plant pathogenic MLOs maintained on periwinkle (*Catharanthus roseus*). Restriction profiles after digestion with endonucleases permit the differenciation of MLOs associated to different plant diseases.

1992 **Boidron and Grenan**: Construction and testing in ENTAV, Le Grau du Roi (France) of a device for secure soaking of dormant buds and canes into hot water (50°C, 45mn).

1992 **Caudwell and Kuszala**: Detection with ELISA of FD-MLO in naturally FD-affected grapevines. Affected grapevines in the Rhône valley tested negative, suggesting an unrelated agent.

1992 **Credi and Santucci**: Of 628 attempts to transmit the agent of a yellows disease of grapevine from Sangiovese, Caveccia and Chardonnay vines to periwinkle by the dodder species *Cuscuta campestris*, 4 positive results (0.6%) were obtained. MLOs were visible in sections of petioles of periwinkle showing symptoms and subsequent graft transmission from periwinkle to periwinkle was successful.

1992 **Daire** *et al*.: First detection of FD-MLO DNA in grapevine extracts by DNA-DNA hybridization with DNA probes cloned from FD-MLO partially purified from experimentally infected plants (*Vicia faba*). The titre of MLO appears very low in grapevine. FD-MLO DNA can be distinguished from other MLO DNA with Dot-blot hybridization and Southern-blotting. It is more related to the agent of Elm yellows than to other yellows agents.

1992 **Davis** *et al*. (a and b): Characterization of Italian periwinkle virescence (IPVR) MLO (obtained on bait periwinkle plants exposed in yellows-affected vineyards in Italy) is possible with DNA-DNA hybridization and PCR. IPVR is related to aster yellows MLO.

1992 **Meignoz** *et al*.: Description of MLOs and associated disorders in the phloem of FD-affected LN33 experimentally inoculated with *S. titanus*. Senescent or degraded forms of MLOs identified inside degenerate sieve elements.

1992 **Osler** *et al*.: ELISA with FD-antibodies permit to detect related antigens in *S. titanus* leafhoppers. However, transmission by feeding to healthy grapevines succeeded only in 1 attempt out of 100, suggesting the presence of two different diseases at least in Veneto and Friuli-Venezia Giulia.

1992 **Quacquarelli and Barba**: Review of the distribution of flavescence dorée and other grapevine yellows in EEC viticultural countries.

1993 **Alma** *et al*.: Transmission experiments from grapevine to grapevine and to herbaceous hosts with *S. titanus* and other leafhopper species show that yellows disease present in northeastern Italy differs from flavescence dorée as it occurs in France.

1993 **Arnò** *et al*.: The survey in Piemonte of Chardonnay vineyards affected with a FD-like disease shows that no correlation can be made between the importance of the *S. titanus* population in vineyards and the rate of spread of the disease.

1993 **Arzone** *et al*. (a and b): Observations supporting the existence of different types of grapevine yellows in northern Italy. Attempts to characterize MLO DNA extracted from insects with molecular methods. One MLO strain transmitted with *Macrosteles quadripunctulatus* appears similar or close to aster yellows MLO.

1993 **Bertaccini** *et al*. (b): Evidence of an association of MLOs with grapevine yellows in Emilia Romagna. The MLO strains found in grapevine are related with aster yellows MLOs, but are different from known aster yellows cluster MLO strains.

1993 **Bianco** *et al*. (a): Differentiation with PCR-RFLP analysis between a MLO related to aster yellows in GY-diseased plants from Lombardia and a MLO related to elm yellows in an affected grapevine in Friuli-Venezia Giulia.

1993 **Boubals** (a): Report on a meeting of the French working group on FD. Evolution of the disease and of its vector in the various viticultural regions of France, results of research, detection (ELISA, genomic tests). FD can be readily distinguished from Bois noir.

1993 **Boubals** (b): A severe epidemic of grapevine yellows occurs in Golan (Israel). Typical symptoms on several cvs. No spontaneous recovery. *S. titanus* is not present.

1993 **Caudwell** *et al.*: FD can be transmitted by symptomless rootstocks. Hot water treatments suppress the transmission to Chardonnay indicators.

1993 **Chen** *et al*.: Construction of serological and molecular detection tools to MLO transmitted to periwinkle with dodder from a yellows-diseased grapevine in Friuli-Venezia Giulia (Italy) (later

called FDU, then GYU phytoplasma) and comparison of specificity and sensitivity of the latter tools to detect phytoplasmas in grapevines in New York and Italy. Detection in non symptomatic *V. riparia* in New York and failure of detection in some symptomatic grapevines in New-York and Italy. GYU was later on characterized by other authors as a phytoplasma belonging to the X-disease (16SrIII) group.

1993 **Daire** *et al*. (a and b): PCR-RFLP analysis of 16S rDNA from MLOs show that 2 different MLOs at least occur in yellows-affected grapevines in France. FD is related to elm yellows and BN is related to stolbur. FD detected in leaves of rootstock 3309C and is also present in samples from Veneto (Italy). BN (stolbur MLO) detected in several regions of Italy and in Israel. A third MLO related to X-disease of *Prunus* detected in a grapevine from New York (USA) and in a periwinkle carrying a grapevine MLO (FDI = FDU) transmitted through dodder in Udine (Italy).

1993 **Girolami and Egger**: Importance of contamination of vineyards and diffusion of Grapevine yellows in northern Italy. Experiments on the use of hot water treatment on planting material, on the effects of pollarding affected vines and of chemical sprays against vectors.

1993 **International Committee of Systematic Bacteriology (ICSB), Subcommittee on the Taxonomy of Mollicutes**: The trivial name MLO is replaced by the term phytoplasma as a consequence of the demonstration by diverse studies that the phytoplasmas represent a monophyletic clade of organisms more closely related to mollicutes than to walled bacteria.

1993 **Kuszala** *et al*.: FD-ELISA method was used on tissues of yellows-affected grapevines from diverse countries. Positive assays obtained only on samples from France and Veneto.

1993 **Maixner** (a, b, c and d): Grapevine yellows (Vergilbungskrankheit) are common in the Moselle and Rhine valley. A MLO has been transmitted to periwinkle with dodder. *S. titanus* is not present. Computer analysis for spatial patterns of diffusion show a non-random distribution and suggest transmission from other vines or from weeds.

1993 **Osler** *et al*. (a and b): Various attempts to transmit FD-like disease in different regions of northern Italy, using insects, graft and dodder. In northeastern Italy, healthy plants protected with plastic screens did not develop symptoms and diseased plants protected with screens showed transient recovery.

1993 **Prince** *et al*.: Diversity of MLOs associated with grapevine yellows and transmitted to periwinkle. Detection in grapevines from Virginia (USA) of MLO related to X-disease. Classification of grapevine MLOs into three RFLP groups: elm yellows (FD from France), aster yellows and X-disease.

1994 **Carraro** *et al*.: Six-year transmission trials of different types of yellows with *S. titanus* to test plants of cvs Perera and Chardonnay in Veneto and Friuli-Venezia Giulia (Italy). Transmission has been obtained only from vines of Veneto. *S. titanus* is present in the Friuli-Venezia Giulia region but no transmission assay has been successful. So, at least two different phytoplasmas are infecting grapevines in Veneto: FD *sensu stricto* (transmitted by *S. titanus*) and a second one, probably transmitted by another insect.

1994 **Credi** (a and b): Observation of MLO in yellows-affected grapevines in northern Italy. Description of pathological changes in phloem of leaves and identification of senescent forms of MLO inside degenerate sieve elements. MLO appear to be in very low titre.

1994 **Daire**: PhD thesis on detection and differentiation with DNA-based methods of the MLO agents of GY diseases in France. Only FD and BN have been identified in naturally affected grapevines. FD belongs to the elm yellows group but is different from elm phytoplasmas. BN belongs to the stolbur group. Specific probes cloned and specific primers designed for PCR amplification of phytoplasma DNA.

1994 **Di Terlizzi** *et al*.: Important outbreak of a yellows disease on local varieties in Apulia (southeastern Italy) and infection of periwinkle as bait plants and with dodder transmission. Electron microscopic observation of MLO in periwinkle and grapevine.

1994 **Maixner**: Demonstration that *Hyalesthes obsoletus* (Auchenorrhyncha: Cixiidae) is a vector of German grapevine yellows (Vergilbungskrankheit).

1994 **Parente** *et al*.: Presence of grapevine yellows in northern Portugal and electron microscopic visualization of MLOs in the phloem tissue of petioles of affected plants.

1994 **Prince** *et al*.: MLOs associated to grapevine yellows in Virginia belong to 2 different groups : X-disease group (16SrIII) and aster yellows group (16SrI). Double infection is reported. Related MLOs were also detected in wild grapevines.

1995 **Arzone** *et al*.: Emphasis on the possible role of weeds as reservoir for MLO in vineyards. Ten weeds were found harboring MLOs with transmission electron microscopy.

1995 **Del Serrone** *et al*. (a and b): Grapevine yellows in Latium (southwestern Italy) are not associated with *S. titanus* which has not been found. Molecular detection of aster yellows-related phytoplasma.

1995 **Egger** *et al*.: Survey of yellows symptoms in an ampelographic collection of 1281 cultivars in Conegliano (Veneto, Italy), with the aim of identifying sources of tolerance or resistance to yellows diseases.

1995 **Fortusini** *et al*.: Six-year survey of evolution of yellows symptoms in a 6-12 year-old vineyard of cv Chardonnay that was never sprayed with insecticides. Consideration on possible resistance and research on interaction of phytoplasma with nepovirus infection.

1995 **Laviña** *et al*.: Identification of BN (stolbur phytoplasma) in Spain.

1995 **Maixner** *et al*. (a): Specific detection with PCR of stolbur phytoplasma in grapevines affected with Vergilbungskrankheit, in the vector *H. obsoletus* and in weeds growing in the vineyard in Germany.

1995 **Maixner** *et al* (b): Detection of a new phytoplasma type related to FD in cv Scheurebe showing symptoms of yellows in Palatinate (Germany).

1995 **Padovan** *et al*. (a and b): Detection of a phytoplasma closer to aster yellows phytoplasma than to elm yellows phytoplasmas in GY-affected vines in Australia

1995 **Sancassani and Posenato**: Simultaneous presence of FD and of other yellows type in vineyards of Veneto. The importance of proper identification of disease type for control measures is emphasized.

1996 **Albanese** *et al*.: Presence and distribution of GY in Sicily. PCR detection of phytoplasma with universal primers.

1996 **Alma** *et al*.: Grapevines from Piemonte (northern Italy) contained several different phytoplasmas. The most frequent belonged to group 16SrI-G (later designated as 16SrXII or stolbur group). One grapevine out of 16 contained a 16SrV (= elm yellows) phytoplasma together with a 16SrI-G phytoplasma.

1996 **Boudon-Padieu** (a and b): Reviews on knowledge and research on grapevine yellows.

1996 **Del Serrone and Barba** (a and b): Monitoring of detection of phytoplasma in the organs of grapevine according to the vegetative state. Detection is also possible during winter on wood scrapings.

1996 **Haidar**: First report of symptoms of yellows on grapevines in Lebanon.

1996 **Koruza**: Dispersal of grapevine yellows in Slovenia, probably of Bois noir type.

1996 **Murari** *et al*.: Four different phytoplasmas (FD, aster yellows, stolbur and apple proliferation) can be detected, sometimes in mixed infection, in grapevines with yellows symptoms in Soave (Veneto, Italy).

1996 **Padovan** *et al*.: The phytoplasma associated with Australian grapevine yellows is close to but different from stolbur phytoplasma causing BN.

1996 **Rüdel**: Review on the history and diversity of Vergilbungskrankheit of grapevine in Germany.

1997 **Batlle** *et al*.: Identification of Flavescence dorée in Spain.

1997 **Belli** *et al*.: History and control of GY diseases in Italy.

1997 **Bosco** *et al*.: Survey of leahoppers in vineyards of Piemonte, northern Italy. Among 32 species identified, 10 are confirmed phytoplasma vectors. Presence of *S. titanus* reported for the first time in this region.

1997 **Daire** *et al*. (a): Only stolbur and FD phytoplasmas were detected in samples of yellows-affected grapevines from numerous regions of France and from Italy, Spain and Israel. Aster yellows and X-disease types were never detected. No double infection has been found to occur.

1997 **Davis** *et al*. (b): Prospects on detection and identification of grapevine phytoplasmas with new molecular tools and consequence on future epidemiology studies.

1997 **Del Serrone** : A review in Italian on the knowledge on etiology, spread, vectors and detection of the agents of Grapevine yellows.

1997 **Garau** *et al*.: Recurrent and severe yellows symptoms observed since the 1980's in Sardinia (Itlay) on several cultivars. No epidemic outbreak has been observed. *S. titanus* is not present. Positive reaction with a DNA probe specific to aster yellows phytoplasmas.

1997 **International Committee of Systematic Bacteriology (ICSB), Subcommittee on the Taxonomy of Mollicutes**: The taxonomy of phytoplasmas will refer to their molecular phylogeny. The term phytoplasma will become the genus name of plant pathogenic mycoplasmas under the provisional taxonomic status *Candidatus*. Subclades are considered to represent the equivalent of distinct species.

1997 **Kölber** *et al*.: Symptoms of grapevine yellows observed in Hungary in the early 1970's. Severe symptoms with high incidence on seven cultivars are reported from four grapevine-growing regions surveyed for 5 years (1993-1996). Phytoplasma belonging to the stolbur subgroup have been identified.

1997 **Maixner and Reinert** (a): Hot water treatment (HWT) of 50°C for 60 min applied to dormant mature canes eliminated Vergilbungskrankheit phytoplasma with a small loss in survival of the cuttings.

1997 **Maixner** *et al*. (a): Description of available methods and strategies for detection of phytoplasmas in grapevine.

1997 **Maixner** *et al*. (b): Survey of possible auxiliaries for the biological control of leafhoppers and planthoppers in vineyards.

1997 **Murari** *et al*.: Use of Hot water treatment (HWT) to eliminate phytoplasmas (FD and AY) from 3 cultivars of grapevine. No positive detection with PCR on the HW-treated vegetative progeny of mature canes of symptomatic plants.

1997 **Tanne and Orenstein** (a and b): Successful heterografting transmission of phytoplasma from symptomatic grapevine to periwinkle and easy subsequent identification of phytoplasma type. AY and X-disease related phytoplasmas have been transmitted and detected.

1998 **Aldini** *et al*.: Survey of hoppers in vineyards of the province of Piacenza (Emilia Romagna, Italy). Among 29 species of Auchenorrhynchas from the vine canopy and weeds of the border, 10 species were known vectors of phytoplasmas. *S. titanus* is not reported.

1998 **Borgo**: Description and colour photographs of symptoms of grapevine yellows and knowledge on their aetiology and vectors.

1998 **Boudon-Padieu and Maixner**: Updating in French and English of present knowledge on grapevine yellows: etiology, transmission, biology and control. The possibilities of control

depend on the knowledge of the biology of phytopathogenic agents and of their vectors. Insecticide sprays against *S. titanus*, vector of FD, are compulsory in France.

1998 **Lee** *et al*.: Phylogenetic studies of phytoplasmas associated to numerous plant diseases. On the basis of RFLP of PCR-amplified 16S rRNA gene, phytoplasmas can be classified into 14 groups and 38 subgroups.

1998 **Maixner and Reinert**: Updating in German of the research made in different countries on grapevine yellows diseases, with a particular reference to the work done in Germany.

1998 **Reinert W. and M. Maixner**: A review of thermotherapy to cure phytoplasma infected material.

1998 **Refatti** *et al*.: Summary of the complex situation of GY in northeastern Italy. Survey with PCR of phytoplasmas infecting grapevines in Friuli-Venezia Giulia and Trento province (Italy) and in Slovenia, have shown that only stolbur group phytoplasma was consistently found. FD-related phytoplasmas (elm yellows group) have been detected in grapevines from Treviso and Verona and transmitted from vine to vine using *S. titanus*. In the Veneto region only stolbur-group phytoplasma was recorded in some areas and both stolbur and elm yellows group phytoplasmas in other areas. In addition a phytoplasma (FDU=GYU) transmitted from GY-affected vines to *Catharanthus roseus* by means of dodder in Friuli-Venezia Giulia, has been identified as a member of the X-disease group.

1998 **Seemüller** *et al*.: A comprehensive review of the classification of phytoplasmas in the world, according to the most recent studies on molecular structure of rDNA, nucleic acid hybridization and serological comparisons. Phytoplasmas for which 16S rDNA sequence is available have been classified into 20 major groups and subgroups. Grapevine phytoplasmas classify into different groups.

1999 **Borgo** *et al*.: Unsatisfactory results on the use of hot water treatments to eliminate phytoplasmas from grapevine wood.

1999 **Boudon-Padieu**: Review on recent progress in the knowledge on grapevine yellows, methods of detection of phytoplasmas in grapevine tissues and in insect vectors, epidemiology of these diseases, distribution in the world.

1999 **Firrao** *et al*.: Monitoring grapevine yellows in North-eastern Italy and attempts to rationalize routine laboratory testing for the differentiation between FD and stolbur phytoplasmas. Sensitivity of assays must be good because of the low titre of phytoplasmas in affected plants.

1999 **Lherminier** *et al*.: First report of the use of oligonucleotides for *in situ* hybridization with transmission electron microscopy to localize phytoplasma in plant cells. Probes were antisense to stolbur specific sequences in the 16S rDNA and used on stolbur-infected periwinkle. Similar attemp with FD phytoplasma were not successful.

2000 **Batlle** *et al*.: A review of the situation of GY in Spain. GY affect mainly the northern provinces. Only FD and BN have been identified. FD is restricted to the north of Cataloña, though *S. titanus* is more widely distributed. BN is very frequent but *H. obsoletus* is rarely found in vineyards. Search for alternative vectors.

2000 **Boudon-Padieu** (b): Chapter in a Handbook on viral and bacterial diseases of the grapevine. History, symptoms, epidemiology and etiology of GYs in the world.

2000 **Carraro** *et al*.: A history of GYs in north-eastern Italy.

2000 **Frausin** *et al*.: Evaluation on the efficiency and security of hot water treatment used to eradicate phytoplasmas from propagation material. No negative effect was observed on scion buds but rootstock cuttings were more sensitive to negative effects of the treatment.

2000 **Guadagnini** *et al*.: Report of positive detection of aster-yellows phytoplasma in grapevine fed with *Metcalfa pruinosa* and in the body of the insects used for transmission.

2000 **Moretti and Anaclerio**: Evaluation of the effects of hot water treatment on the viability of grapevine cuttings of different varieties with different temperature / time combinations. Plant variety and cutting diameter influence the rate of surviving cuttings.

2000 **Zahavi** *et al*.: Survey of GY in Israel. Influence of rootstock on the rate of GY symptoms in the same vineyard and same grapevine variety. A high rate of recovery is observed from one year to the next. The phytoplasma agents are not specified.

2001 **Bertaccini** *et al*.: Use of immersion in hot water (HWT) or in chemicals to suppress phytoplasmas from grapevine propagation material in Italy. HWT (50°C/40 mn) gave acceptable survival but none of the conditions experimented provided a total elimination of phytoplasmas. The latter was difficult to evaluate because of the non homogenous distribution of phytoplasmas in canes.

2001 **Bertamini and Nedunchezhian**: Study of the effect of phytoplasma infection of field-grown plants of cv Chardonnay affected with Bois noir (stolbur phytoplasma) on the physiological response of plants: photosynthesis, sugar metabolism, nitrate and nitrite reductase.

2001 **Clair** *et al*.: *Metcalfa pruinosa* specimen reared in the laboratory may acquire FD and clover phyllody (aster yellows group) phytoplasmas by feeding on infected *Vicia faba* but feeding transmission to several plant species has not been obtained. Phytoplasmas seemed to disappear from the insect body after the transfer of insects to healthy plants, suggesting that they did not multiply in the body of the insects.

2001 **Klein** *et al*.: In Golan Heights (Israel) *Hyalesthes obsoletus, Neoaliturus* sp., *Circulifer* sp. *Macrosteles quadripunctulatus* and *Orosius orientalis* were found on weeds in vineyards or trapped on sticky traps. Phytoplasmas were detected in all five species, which are all known as vector of phytoplasmas.

2001 **Marzachi** *et al*. (a): Presence of FD, BN and aster yelllows in vineyards of southeastern Piemonte (Italy).

2001 **Orenstein** *et al*.: A 2-year survey in Golan Heights, Israel, confirmed the presence of three phytoplasmas associated to GY: stolbur (70%), aster yellows (11 %) and X-disease groups phytoplasmas. Dual infection may occur (13 %). Primers fitted for specific detection of these 3 phytoplasmas permit cheaper and quicker diagnosis.

2001 **Quartau** *et al*.: *Scaphoideus titanus* is present in Portugal.

2001 **Seljak and Petrovic**: Overview on phytoplasma diseases of grapevine and fruit trees in Slovenia. FD has not been identified, although its vector *S. titanus* is widespread in western vineyards. *Hyalesthes obsoletus* has been found but not in vineyards.

2001 **Tanne** *et al*.: The presence of phytoplasmas in liquid medium on which insect vectors have been fed can account for potential vectorship of the species. Experimental evaluation of the method and application to field-trapped individuals of suspected vector species.

2001 **Waite** *et al*.: Use of hot water treatment in commercial nurseries in Australia to eradicate diverse pests and pathogen agents from propagation material.

2002 **Crocker** *et al*.: Recommandations for the organisation of nursery in Australia and handling of hot water treatment to avoid dehydration of cuttings during treatment.

2002 **Frosini** *et al*.: Development of a new technique with DNA chips to detect phytoplasmas in grapevine.

2002 **Moretti** *et al*.: Report of experiments combining temperature and time of treatment with hot water on 5 grapevine cultivars to cure planting material from phytoplasmas.

2002 **Osler and Refatti**: The situation of GYs in northern Italy.

2002 **Seljak:** A review of non-European hoppers introduced in Slovenia.

2003 **Boudon-Padieu**: Updating of knowledge and research on grapevine yellows worldwide.

2003 **Boudon-Padieu** *et al*.: Compared efficiency, rapidity and sensitivity of methods for use in routine diagnosis of grapevine phytoplasmas.

2003 **Chabbouh** *et al*.: Identification of grapevine yellows symptoms in Tunisia and attempts to identify pathogen agent and vector. An aster yellows phytoplasma is suspected.

2003 **Clair** *et al*.: Development of a sensitive PCR procedure for dual identification of FD and BN phytoplasmas, fitted to routine detection.

2003 **Crocker** *et al*.: Measurements of basal respiration rate of grapevine dormant wood as an indicator of the best period for application of hot water treatment.

2003 **Gajardo** *et al*.: Identification of aster yellows (16SrI-B and C) and of ash yellows (16Sr-VII) related phytoplasmas associated to yellows of grapevine in Chile.

2003 **Ge and Maixner** (a): Transmission to feeding medium is more efficient than transmission to natural host plants and to grapevine for *Hyalesthes obsoletus* and *Oncopsis alni*, two nonpreferentially ampelophagous vectors of grapevine phytoplasmas. Discussion on benefits and limits of artificial feeding medium to assess the transmission capability of phytoplasma by insects.

2003 **D'Ascenzo** *et al*.: Important presence of GY in Abruzzo (central Italy). BN (stolbur phytoplasma) has an incidence of about 30 %. Other phytoplasmas are reported, in particular a clover phyllody type (16SrI-C) which is quite frequent.

2003 **Duduk** *et al*. (a and b): FD phytoplasma (16S rV-C) and *S. titanus* found associated to grapevine yellows with a high incidence in vineyards of Rastina (South Serbia).

2003 **Kuzmanovic** *et al*.: Report of severe symptoms of yellows on numerous grapevine varieties in Serbia and observation of organisms resembling phytoplasmas in sieve tubes of affected shoots collected in the Zupa area. Apart from FD phytoplasma reported by Duduk *et al.*, stolbur phytoplasmas are suspected to occur because of long-lasting record of stolbur disease on many host plants in Serbia.

2003 **Lessio** *et al*.: Flight activity of *Scaphoideus titanus* and *Hyalesthes obsoletus* and their infection status towards FD and BN (stolbur) phytoplasma, respectively.

2003 **Marzachi** *et al*.: Improvement of detection of FD and BN in field-grown grapevines with real-time PCR.

2003 **Myrta** *et al*.: Report of stolbur phytoplasmas in grapevine affected with yellows in Albania.

2003 **Orenstein** *et al*.: Survey of potential vectors of phytoplasmas in vineyards of the Golan Heights. *Neoaliturus fenestratus, Hyalesthes obsoletus* and *Circulifer haematoceps* abundant and positive for stolbur and aster yellows phytoplasmas. *Megophthalmus scabripennis* positive for aster yellows phytoplasma. Study of the spatial and temporal dispersion of the four species.

2003 **Osler** *et al*.: Grapevines affected with yellows are found free of phytoplasmas after recovery. Recovery is a progressive phenonenon developing over 3 years in the case of BN. Consequently roguing of affected vines should be avoided when possible and especially if vectors are controlled.

2003 **Tassart-Subirats** *et al*.: Data on 15-year studies on efficiency and effect on propagation material of hot water treatment.

2004 **Leitner**: The situation of Grapevine yellows in Austria is now surveyed by means of molecular detection assays. No important damage has been reported.

2004 **Milkus** *et al*.: Important outbreak of grapevine yellows on cv Chardonnay and identification of a stolbur phytoplasma in diseased plants.

2004 **M'hirsi** *et al*.: Report of aster yellows phytoplasmas in grapevine affected with yellows in Tunisia.

GRAPEVINE YELLOWS: INDIVIDUAL DISEASES

A. FLAVESCENCE DORÉE

1. Description

Flavescence dorée (FD) was the first Grapevine yellows (GY) disease to be reported. It is highly epidemic and extremely dangerous because of the biology and ethology of its leafhopper vector, *Scaphoideus titanus* Ball (= *S. littoralis* Ball). In France, it occurs in all southern vine-growing regions, Corsica, and Savoie. In addition, isolated infected vines have been identified in northern vineyards of Burgundy and Alsace. It was described in a limited area in north-eastern Cataluña (Spain). It is widespread in all northern provinces of Italy and an outbreak was recently reported from southern Serbia.

Main symptoms: It is believed that vines that show symptoms for the first time in a vegetative season had been infected in the previous summer. Symptoms develop on leaves and shoots in June and July to become oustanding in August and autumn. Leaves persist longer on affected plants. Lignification of the canes is usually incomplete. Most of the time, symptoms affect the whole plant. Diseased vines have a patchy distribution in the plot, indicating a vine-to-vine transmission, with an incidence that increases rapidly from one year to the next. Crop losses may be very high.

Affected vines of most varieties may recover in the second year when they are protected against re-inoculation with insecticide treatments. If the plants are inoculated after recovery, symptoms may be limited to a few shoots. However, extremely sensitive varieties do not recover, decline progressively and die.

Infected rootstocks show little or no symptoms. However, rooted cuttings from infected canes of a few rootstock varieties can develop "vinifera-like" symptoms on the wood and leaves, show a general asymmetric bent posture and necrosis of terminal bud.

Agents: FD was first regarded as a physiological disorder, then as a virus disease. The associated phytoplasma (= MLO) was observed in phloem tissue of affected plants and in insect vectors in 1971 and later classified in the Elm yellows group (16SrV). After the discovery of other GY diseases, the term "FD *sensu stricto*" was applied to diseases and phytoplasmas that are transmitted by *S. titanus.* Several isolates have been characterized with molecular criteria. Isolates F70, FD88, FD92 and FD2000 were experimentally transmitted to broadbean (*Vicia faba* L.) using *S. titanus* individuals collected in infected vineyards of south-western France. These isolates could be distinguished by Western-blot analysis using FD antisera and monoclonal antibodies (Mabs). Two isolates denoted FD-D and FD-C, were characterized in Italy and shown to be transmitted also by *S. titanus*. Molecular comparisons have shown that all these isolates are more closely related among them than with other phytoplasma strains in the same group. Moreover, FD88, FD92 and FD-D could not be distinguished from one another.

Transmission: The FD agent is transmitted in the persistent mode by the leafhopper *Scaphoideus titanus* Ball (= *S. littoralis* Ball) (Homoptera, Cicadellidae). FD is endemic only in regions where *S. titanus* is well established. This leafhopper is a neartic species specialized on *Vitis* sp. introduced into Europe at the beginning of the 20th century, that has colonized a wide climatic area. It is also present in regions from which FD has not been reported in France, Switzerland, north of Spain and Portugal, southern Italy, and western Slovenia. Vineyards in these areas are under the threat of an FD outbreak that could occur if FD-infected planting material is introduced. *S. titanus* is a univoltine species that overwinters at the egg stage and develops from May to September on grapevine leaves with 5 aerial apterous larval instars followed by alate nymphs that feed on the leaf veins and petioles and on green shoots. Eggs are laid in summer on two-year old wood and trunk. Phytoplasma acquisition by all insect instars (larvae and nymphs) may occur from infected vines at any time from the beginning of hatching (usually in the beginning of May) throughout the growing season. Feeding transmission starts after a 4-week latency in the body of the vector. Hence, transmission is possible from early June (about one month after the beginning of hatching) until the death of adults.

Transmission occurs also by vegetative propagation and grafting. Infected buds or graftwood may be collected from symptomless parts of infected mother vines or from recently infected vines that have not yet developed symptoms. Infected rootstocks are important means of dissemination because they are symptomless. Though the rate of transmission by bench grafting can be very low, this way of spreading is significant when infected grafted plants are planted in vineyards hosting the vector. First symptoms may

appear on young vines as late as four years after grafting. The low rate of transmission by grafting and the long delay in symptom expression make the detection of infected vines in planting material difficult, and the risk of disease spreading important.

Varietal susceptibility and sensitivity: All varieties grown in the various FD-affected regions in France, Italy and Spain are susceptible with various degrees of sensitivity. Nielluccio and Garganega are very sensitive varieties that usually do not recover after infection. Alicante Bouschet, Grenache, Cabernet Sauvignon, Sauvignon blanc, Chardonnay, Ugni blanc (Trebbiano) and Prosecco are sensitive varieties that may recover when they are protected from new inoculations. Other varieties, such as Merlot, appear more tolerant, although heavily infected vines can be observed. Symptoms are rare in Syrah. *Vitis riparia* can be infected but shows little symptoms. The same is true for American rootstocks which can therefore be dangerous sources of infection and dissemination of the disease.

Other host plants: No host plants other than *Vitis* sp. have been found carrying FD phytoplasma until recently. In 2003 a phytoplasma resembling the FD-C isolate was found in wild Clematis in Veneto (Italy).

Detection: FD symptoms can be confused with those of other GYs and also with other diseases or disorders. The presence of *S. titanus* in an affected vineyard is an important indication that may lead to suspect a FD infection. Nevertheless, Bois noir (BN) is also frequent in regions inhabited by this leafhopper.

Detection with laboratory methods is possible on insect vectors and infected vines. Polyclonal antisera and Mabs have been raised to FD phytoplasma. Antigen extraction from vascular tissue of symptomatic grapevines requires the use of high Tris molarity and strong detergents in the extraction buffer. An indirect DAS-ELISA using coating of wells with rabbit polyclonal antisera and detection with a cocktail of several Mabs, has been used as the official method for large scale survey of FD in France from 1993 to 2003.

Molecular detection by PCR of selected phytoplasma DNA fragments, has become the preferred detection method because it is easy to perform and was improved in reliability and sensitivity. Nested PCR and RFLP analysis of selected fragments of the 16S rDNA permit the characterization of any phytoplasma and especially to differentiate FD from BN. Recently, sensitive amplification with nested PCR of the DNA fragment FD9, which is specific for 16SrV-group phytoplasmas allowed the reliable detection of FD phytoplasma in grapevine. Simultaneous amplification in a multiplex procedure of both FD9 and Stol11, a DNA fragment specific to BN (stolbur) phytoplasma can be used for the survey and monitoring of these two GY diseases. Sequence or RFLP analysis of the FD9 DNA fragment permit to readily differentiate all the known FD isolates.

Other DNA-based methods, such as real-time PCR or identification of PCR-amplified product with DNA-DNA hybridization using specific probes, are currently under development.

Control: FD is a quarantine organism in the EC. In France and Italy, control measures are compulsory according to legal regulations. Indirect control is obtained by insecticide treatments against *S. titanus*. Natural insecticides can be used to preventively limit vector populations but their efficiency is limited in epidemic outbreaks. Under these circumstances only chemical insecticides are efficient for eradication of the disease. The first treatment is applied 30 days after first instar emergence at the beginning of the period of potential transmission. Two additional treatments are applied during summer. The second treatment, at the beginning of July, aims at killing newly hatched insects, whereas the third treatment, at the beginning of August, is directed against winged adults migrating from nearby vineyards or wild vines. Monitoring natural enemies of *S. titanus* in New York State (USA), its area of origin, has allowed the identification of potential auxiliaries for biological control. Their rearing is still under development.

In spite of the possibility of recovery, roguing of diseased vines is advisable when the epidemic pressure is high. Roguing is compulsory in France.

Planting material must not be collected from mother vines in areas or vineyards affected by the disease. In France and Italy budwood can be taken only from mother plants growing in plots that have shown no GY symptoms for the last two growing seasons. Material from mother plants that have developed symptoms in the following growing season, must be destroyed. Soaking of dormant material in hot water (HW) is recommended. Standard conditions (50°C for 45 min) proved highly efficient for sanitizing infected rootstocks and grapevine cultivars. Planting of HW treated material is especially important in areas where the vector is present.

2. Historical review

1955 **Levadoux**: Description of an outbreak of "Flavescence dorée" on Baco 22A in southwestern France. The aetiology is unknown.

1956 **Branas** (a and b): The new disease is thought to be caused by root damage.

1957 **Caudwell**: The disease is denoted Flavescence dorée (FD) in agreement with the name proposed by Levadoux (1955) because of the golden yellow metallic aspect of the leaves. Description of macroscopic and microscopic symptoms, evolution of the disease in space and time. The disease can be transmitted by grafting and has probably a viral aetiology.

1960 **Bonfils and Schvester**: Relationships of leafhoppers with FD of grapevine in western France.

1960 **Caudwell and Poitou**: Study of the interaction between fanleaf and FD.

1961 **Caudwell**: Study of the phenomenon of recovery of FD-affected vines. Spontaneous recovery occurs after a 1-2 year crisis period. Recovered vines may be infected again but the symptoms are lighter.

1961 **Schvester** *et al*.: Demonstration that FD is transmitted by the leafhopper *S. littoralis* Ball, an insect recently introduced from North America.

1962 **Schvester** *et al.* (a): Control of FD by insecticide treatments against the vector, *S. littoralis.* Use of 4-5 treatments with DDT or parathion and removal or destruction of pruning wood older that two years. First report that abandoned or wild vines may be a source of infection.

1962 **Schvester** *et al*. (b): Biology of *S. littoralis*.

1963 **Schvester** *et al*.: Field tests for insecticide control of *S. littoralis*.

1964 **Caudwell**: PhD thesis on FD, considered as a virus disease. Description and study of recovery phenomenon and of localised symptoms.

1964 **Vidano**: *S. littoralis* recorded from in Italy in 1963. Description of the insect, biology and feeding damage and of the symptoms of FD in France on Baco 22A.

1966 **Caudwell**: Attempts to inhibit the agent of FD *in vivo* by heat treatment. Immersion in lukewarm water (30°C) for 72 h of cuttings from FD-affected grapevines reduced the proportion of infected plants by about 83 % as compared with untreated control.

1966 **Vidano**: Study of the ecology and biology of *S. littoralis* in its area of origin in North America.

1967 **Carle and Moutous**: Study on possible secondary or alternative vectors of FD or Bois noir (BN). No positive results of transmission trials with 15 species of Hemiptera (mainly Cicadellidae) other than *S. littoralis.*

1968 **Baggiolini** *et al*.: First report of *S. littoralis* from Ticino (southern Switzerland).

1969 **Caudwell** *et al*.: Studies on the survival of *S. littoralis* on plants other than the grapevine and transmission trials of FD to other host plants.

1970 **Caudwell** *et al*.: Successful transmission of FD to herbaceous hosts by increasing the feeding access period of the vector *S. littoralis.*

1971 **Boubals and Caudwell**: FD epidemics observed in Corsica. *S. littoralis* is present.

1971 **Caudwell** *et al*. (a). Study of the role in the aetiology of FD of mycoplasmalike organisms (MLO) observed in insect vectors and in inoculated grapevine and *V. faba* plants.

1972 **Caudwell** *et al*. (a): Possibility to limit the populations of *S. littoralis* in Corsican vineyards with winter treatment of dormant eggs with oleoparathion.

1972 **Caudwell** *et al*. (c): Transmission of FD from *Vicia faba* to *V. faba* by leafhoppers of the genera *Euscelis* and *Euscelidius* and from *V. faba* to grapevine by *S. littoralis*.

1972 **Caudwell** *et al.* (d): Different damage caused by leafhoppers in vineyards and specific control of *S. littoralis*.

1973 **Belli** *et al*.: A disease similar to FD observed in vineyards of Oltrepò Pavese since 1968.

1974 **Caudwell** *et al*.: Research on liquid media to preserve and cultivate MLO agents of FD. Use of the infectivity test to evaluate MLO survival or multiplication.

1975 **Osler** *et al*.: *S. littoralis* found in vineyards of Oltrepò pavese affected with a FD-type disease.

1977 **Caudwell and Larrue**: Rearing of colonies of healthy and MLO-infected leafhoppers.

1977 **Moutous** *et al*.: Results of ovicide treatments against *S. littoralis*.

1978 **Caudwell** *et al*.: Successful transmission with *S. littoralis* of the Corsican GY, thus identified as the same disease as FD.

1979 **Caudwell and Larrue**: The problem of FD in France in relation with sanitary selection of grapevine planting material.

1982 **Caudwell** *et al*.: Use of serology for detecting FD MLOs by immunosorbent electron microscopy. Antisera raised to MLOs extracted from *E. variegatus* are used to trap MLOs in extracts from *V. faba*.

1984 **Belli** *et al*.: Presence of *S. titanus* (= *S. littoralis*) in vineyards of the Veneto (northern Italy) and spread of FD in this region.

1985 **Anonymous**: An important outbreak of FD observed in South France since the beginning of the 1980's. The situation is critical.

1985 **Belli** *et al*. (a): FD, which was reported in Italy for the first time in 1973, is now spreading northeast in the Veneto region. The vector *S. titanus* is abundantly present.

1985 **Belli** *et al*. (b): Problems of identification of FD in Veneto (Italy) and correlation with the presence of the vector.

1986 **Bagard and Felici**: The situation of FD in Corsica is very serious.

1986 **Boudon-Padieu and Larrue**: ELISA detection of FD MLO is possible in leafhopper vectors reared in the laboratory and in *S. littoralis* individuals trapped in FD-affected vineyards. Positive insects were found in South-eastern France.

1986 **Kuszala**: Injection of MLO-enriched extracts into the body of *Euscelidius variegatus* is used for evaluating the infectivity of the extracts. Males are better vectors than females.

1987 **Agulhon and Laurent**: Biology and spread of *Scaphoideus titanus* (= *S. littoralis*) in vineyards of the south of France.

1987 **Borgo** (a and b): Study on the susceptibility and tolerance of grapevine cultivars in Veneto.

1987 **Boudon-Padieu** *et al.* (a and b): Development of serological assays (ELISA, Immunofluorescence and Western-blotting) for the detection and characterization of FD-antigens in infected leahopper vectors.

1987 **Caudwell** *et al.:* Present knowledge on the biology, aetiology and diagnosis of FD MLO.

1987 **Pavan** *et al*.: Dynamics of the populations of *S. titanus* in Veneto.

1987 **Planas**: Report on field trials to control FD and its vector in South France.

1987 **Seljak**: Presence of *S. titanus* in Slovenia (western Yugoslavia).

1989 **Anonymous**: Compared efficiency of various insecticides in the control of *S. titanus.*

1989 **Boudon-Padieu** *et al*. (a and b): Polyclonal antisera raised to FD MLO maintained in the laboratory permit detection in infective *S. titanus* individuals from affected vineyards. Description of the infection cycle of the MLO in the body of the experimental vector *E. variegatus*.

1989 **Du Fretay** *et al*.: Satisfactory control of the vector of FD in 1988 in South France.

1989 **Fortusini** *et al*.: Successful transmission of FD to grapevine cuttings using *S. titanus* in Italy.

1989 **Laurent and Agulhon**: 1989. Comprehensive review of the situation and evolution of FD and the vector leafhopper in French wine-growing regions.

1989 **Lherminier** *et al*.: *In situ* detection of FD MLO in salivary glands of infective *Euscelidius variegatus* leafhoppers with immunofluorescence.

1989 **Schwartz**: PhD thesis on the production, screening and characterization of monoclonal antibodies to the FD-MLO.

1990 **Boudon-Padieu** *et al*.: Serological differentiation between FD-MLO and Phy-MLO, an agent causing phyllody in *V. faba* plants, transmitted in the laboratory by *Euscelidius variegatus* leafhoppers.

1990 **Caudwell** *et al*.: Hot water treatment to disinfect grapevine wood from FD-MLO.

1990 **Lherminier** *et al*. (a and b): The use of immunolabeling in the electron microscope to detect and localize MLO in plants and insects with specific polyclonal antibodies.

1991 **Arzone** *et al*.: Electron microscopic observation of MLO in sieve elements of Chardonnay and Perera grapevines showing FD symptoms, in clover (*T. repens*) inoculated with *S. titanus* fed on infected grapevines and in salivary glands of the leafhopper.

1991 **Cazenove and Planas**: Attempts to obtain a satisfactory control of *S. titanus* with natural insecticides used in biological agriculture.

1992 **Anonymous**: Recommendations for control of FD in biological wine-growing. Combination of winter treatments with white oil and removing of pruning wood to suppress eggs.

1992 **Caudwell and Kuszala**: ELISA detection of FD MLO in affected grapevines. The method requires extraction of proteins with a strong detergent. DAS ELISA is developed with polyclonal rabbit antiserum as coating antibodies and a cocktail of mouse monoclonal antibodies as detecting antibodies.

1992 **Daire** *et al*.: Random cloning of FD-MLO DNA and selection of specific probes for detection of FD MLO with DNA-DNA hybridization. Detection in field-infected grapevines is possible only on DNA extracted from a MLO-enriched fraction.

1992 **Jermini** *et al*.: In spite of the presence in Ticino (Switzerland) of *S. titanus* in vineyards and nurseries, FD does not seem to occur.

1992 **Lozzia**: A review of the presence, biology and control of *S. titanus* in Italy.

1992 **Meignoz** *et al*.: Electron microscopic study of the cytopathogenic effects of FD-MLO in experimentally infected cuttings of LN33.

1992 **Osler** *et al*.: *S. titanus* fed on yellows-diseased grapevines in northern Italy (Friuli-Venezia Giulia), test positive to FD-antibodies raised in France.

1993 **Caudwell** *et al*.: Positive indexing of rootstocks showing latent FD infection and erratic distribution of the pathogen in the material. Sanitation of rootstocks with hot water treatment (50°C for 45 mn).

1993 **Daire** *et al*. (a and b): Diversity among MLOs inducing GY diseases in France and other countries, shown with PCR-RFLP analysis of rDNA. FD shows the same pattern as elm yellows MLO. BN is related to stolbur MLO. FD MLO was detected in samples from France and Veneto (Italy).

1993 **Jermini** *et al*.: Assessment of the optimal number and disposition of sticky traps to evaluate the importance of *S. titanus* populations in the vineyard.

1993 **Lefol**: PhD thesis on recognition between the FD-MLO and the organs of the experimental leafhopper vector *Euscelidius variegatus*.

1993 **Lefol** *et al*.: Development of the "double-dot" method and a derived procedure in the transmission electron microscope to identify the sites of attachment of the FD-MLO on insect organs in vector and non-vector insect species.

1993 **Maixner** *et al*.: Study of *S. titanus* in New York and its possible relationship to an American GY. *S. titanus* transmitted a yellows disease to 29% of *Vicia faba* plants. FD antibodies raised in France tested positive on 13% of American *S. titanus* individuals.

1993 **Seddas** *et al*. (a and b): Immunoaffinity purification of FD-MLO from infected experimental vectors.

1994 **Carraro** *et al*.: Demonstration with transmission trials using *S. titanus*, ELISA and PCR analyses, that FD *sensu stricto* is present in Veneto and not in Friuli-Venezia Giulia, though *S. titanus* is also present in the vineyards of the latter region.

1994 **Caudwell** *et al*.: Identification of latent FD infection in several rootstock varieties, including 3309 Couderc and Fercal. The rate of graft transmission to scion depends on the infection status of mother vines and could reach 80 %.

1994 **Farmer and Boudon-Padieu**: Cloning of FD-MLO DNA, construction of an expression library and screening with FD antibodies allowed the selection of three inserts carrying information for FD membrane proteins.

1994 **Lefol** *et al*.: Route and multiplication of the FD-MLO in the body of experimentally infected *Euscelidius variegatus*. All main organs were infected, except for germinal cells.

1994 **Lherminier** *et al*.: Use of ELISA and immunolabeling by transmission electron microscopy for studying the distribution and movement of FD-MLO in the experimental host plant *Vicia faba*.

1994 **Seddas**: PhD thesis on the production and use of monoclonal antibodies to identify the main antigens of FD-MLO and obtain highly purified fractions of the infectious agent from vector insects and herbaceous host plants.

1995 **Bertaccini** *et al*.: Presence of phytoplasmas of two types, sometimes in double infections, in severely GY-affected grapevines in Liguria (North-western Italy). One type is related to elm yellows phytoplasma and the other to IPVR phytoplasma, shown later on to belong to the stolbur group.

1995 **Seddas** *et al*.: Immunoaffinity purified FD phytoplasmas appear as whole cells in ISEM. Experimental vectors (*E. variegatus*) injected with purified fractions of FD phytoplasma supported its multiplication and were able to feed-inoculate *V. faba* seedlings.

1996 **Alma** *et al*.: In Piemonte, several phytoplasmas were identified in yellows-affected grapevines. A 16SrV (= elm yellows) phytoplasma was detected in a double infection with a 16SrI-G phytoplasma. Phytoplasmas of the latter group (later renamed 16SrXII = stolbur) were the more numerous.

1996 **Bianco** *et al*. (a and b): Elm yellows-related (16SrV) phytoplasmas are present only in the Vicenza and Arezzo provinces of northern Italy. Two different RFLP patterns can be distinguished, suggesting the existence of two strains of FD phytoplasma, one of which is similar to the French strain.

1996 **Borgo**: The first occurrence of FD *sensu stricto* in the province of Treviso (northern Italy) was reported in the 1980's. Infection is rapidly spreading to the east.

1996 **Jermini and Baillod**: Combination of visual observation of instar larvae and trapping of adults on sticky traps to monitor the populations of *S. titanus* in Switzerland.

1996 **Kuszala**: Specific ELISA procedures to detect FD or BN phytoplasmas in extracts from diseased grapevines from the field.

1996 **Lherminier and Boudon-Padieu**: Use of transmission electron microscopy with *in situ* immunolabeling to detect FD phytoplasma in grapevine and herbaceous host plants.

1996 **Posenato** *et al*. (a and b): Situation of FD and *S. titanus* in north-eastern Italy where vines are trained in the pergola system. Survey of hemipters in the vineyard and presence of other known phytoplasma vector species.

1996 **Seddas** *et al*.: Monoclonal antibodies raised to immunoaffinity purified FD phytoplasmas. Several different peptides from membrane proteins are identified by Western-blot. Serological relationships with elm yellows phytoplasma is confirmed

1997 **Alma** *et al*.: A phytoplasma of the 16SrI (aster yellows) group is detected in eggs, nymphs and adults of *S. titanus* reared on healthy plants. The biological significance of this finding is unknown.

1997 **Batlle** *et al*.: First report of FD outbreak in northern Cataluña (Spain).

1997 **Bosco** *et al*.: Monitoring of leafhoppers in vineyards in Italy. Numerous species identified. The possible role of six species in the transmission of GY is discussed.

1997 **Caudwell** *et al*.: Verification of hot water treatment conditions to suppress FD phytoplasma infection in dormant wood of grapevine. In the same conditions, the eggs of *S. titanus* laid in the bark were killed.

1997 **Clerc** *et al*.: First report of *S. titanus* in the canton of Geneva (Switzerland).

1997 **Daire** *et al*.: Development of specific PCR primers for the detection of FD or BN phytoplasmas. The amplified FD9 fragment is specific and variable among 16SrV (elm yellows) group phytoplasmas. Three different RFLP patterns at least are shown in FD isolates from France, Spain and Italy.

1997 **Marcone** *et al*.: RFLP studies of 16SrV phytoplasmas. FD is not present in southern Italy.

1997 **Pavan** *et al*. (a and b): Evolution of FD in the Treviso province (Veneto, Italy). First outbreak in the 1980's on cv Perera. Increase and spread to other cultivars, especially Prosecco in the period 1993-1996. Control recommendations. Transmission by grafting is studied. The possibility that direct inoculations have occurred in nursery is discussed.

1997 **Rousseau**: A review of different ways to reduce the populations of *S. titanus* in biological viticulture.

1997 **Vindimian** *et al*.: In spite of the presence and rapid spread of *S. titanus* in Trentino (Italy), FD has not been identified.

1999 **Martini** *et al*.: Demonstration that two isolates of FD *sensu stricto* (FD-D and FD-C) are spreading in Veneto (Italy).

1999 **Mori** *et al*.: Insecticide control of *S. titanus* in Italy, according to the severity of the FD epidemics.

2000 **Belli** *et al*.: Important outbreak of FD in Lombardia (northern Italy).

2000 **Bianco** *et al*. (a and b): Demonstration of curing effect of hot water treatment on FD-affected plant material.

2000 **Boudon-Padieu** (a): Description, biology, spread, FD-transmission and control of *S. titanus*.

2000 **Clair** *et al*.: Design of internal nucleotides on the specific DNA fragment FD9 to be used as primers in nested-PCR for improving sensitivity of detection of elm yellows (16SrV) phytoplasmas in FD-affected grapevine or in elms affected with yellows in France.

2000 **Cravedi and Aldini**: Biology of *S. titanus* in Oltrepò pavese (Italy), a region affected by a severe outbreak of FD since 1999.

2000 **Morone** *et al*.: Occurrence of FD in Piemonte (northern Italy) since 1998.

2000 **Roure**: The situation of FD in France. Compulsory control (insecticide sprays and roguing of affected vines) on 300 000 ha.

2000 **Scattini** *et al*.: Important spread of FD in Lombardia (Italy) in cv Sangiovese.

2001 **Angelini** *et al*.: Phylogenetic comparison of FD isolates from France and Italy among them and other 16SrV (elm yellows) strains. One isolate from France (FD92 = FD88) and one from Italy (FD-D) are widespread and identical.

2001 **Bianco** *et al*.: *S. titanus* in northern Italy can transmit different grapevine isolates of 16SrV (elm yellows) phytoplasmas.

2001 **Credi** *et al*.: Detection of FD in grapevine samples from the provinces of Piacenza, Parma, Reggio Emilia and Modena in Emilia Romagna (Italy).

2001 **Davis and Dally**: A new 16S rDNA sequence of FD is produced and it is proposed that FD phytoplasmas are placed in two distinct subgroups. However, further work has shown that the 1994 original sequence was erroneous (see Angelini *et al*., 2003a).

2001 **Harrison** *et al*.: An elm yellows (16SrV) group phytoplasma close to the Italian isolate FD-C is detected in Virginia creeper plants (*Parthenocissus quinquefolia*) in southern Florida (USA). It is the first time that a phytoplasma resembling a FD phytoplasma is found in a plant species other than *Vitis* sp.

2001 **Marzachi** *et al*. (b): Development of a PCR strategy for large scale detection of FD phytoplasma in plants and insects.

2001 **Pasquini** *et al*.: Harmonization of procedures for diagnosis of FD in Italy.

2001 **Quartau** *et al*.: Presence of *S. titanus* in Portugal.

2002 **Alma**: A review of the distribution and biology of *S. titanus* in Italy.

2002 **Bianco** *et al*.: Development of a specific TaqMan® assay for detection of FD phytoplasmas.

2002 **Borgo and Angelini**: Spread of FD in Italy and the situation of mother vines and cultural practice.

2002 **Boudon-Padieu**: Present knowledge on the epidemiology, aetiology and diagnosis of FD.

2002 **Credi** *et al*. (b): Presence of FD in the Marche region (central Italy).

2002 **Martini** *et al*.: Further comparisons between FD phytoplasma isolates from France and Italy.

2002 **Mori** *et al*.: Positive transmission of the two Italian FD isolates (FD-D and FD-C) by *S. titanus.*

2002 **Posenato** *et al*.: Efficiency of various insecticides to destroy nymphs of *S. titanus* and *Metcalfa pruinosa*.

2002 **Viggiani**: Presence of *S. titanus* in the Basilicata region (southern Italy).

2003 **Angelini** *et al*.: Use of Heteroduplex Mobility Assay and full sequencing on two genomic DNA fragments (ribosomal and non ribosomal) to further study the relationships between FD isolates and related 16SrV (elm yellows) group phytoplasmas.

2003 **Bianco** *et al*. (b): Presence of FD-D and FD-C isolates of FD phytoplasma in Lombardia (northern Italy).

2003 **Botti and Bertaccini**: Molecular variability between FD phytoplasma isolates using the 16S rRNA gene, the ribosomal protein operon and the FD9 DNA fragment. Distinction between epidemic and non epidemic isolates.

2003 **Bressan** *et al*.: An attempt to identify a pattern of seasonal transmission of FD, taking into account the transmission efficiency of *S. titanus*, the pattern of symptom expression by infected grapevines, the emergence of nymphs of *S. titanus* and the importance of vector population and diseased grapevines.

2003 **Cavallini** *et al*.: Presence of FD together with BN in the area of Modena (north central Italy).

2003 **Clair** *et al*.: A multiplex nested-PCR procedure for easy simultaneous diagnosis of FD and BN. The method is now the official method registered in the Official Journal of the French Republic to be used by laboratories in the frame of compulsory control of FD in vineyards.

2003 **Constable and Boudon-Padieu**: Isolation of FD phytoplasma chromosome in Pulse Field Gel Electrophoresis and first physical map for two FD isolates.

2003 **De Sousa** *et al*.: Identification of FD-D phytoplasma in *S. titanus* specimen trapped in Portugal. No description of FD-affected grapevines.

2003 **Duduk** *et al*. (a and b). Identification of FD in southern Serbia and presence of *S. titanus*. The phytoplasma isolate is similar to FD-C.

2003 **Malausa** *et al*.: Search for natural enemies of *S. titanus* in New York with the scope of their introduction in France as biological control auxiliaries.

2003 **Nusillard** *et al*. Results of a 2-year study in North America of the natural enemies of *S. titanus*.

2003 **Santinelli** *et al*.: Presence of *S. titanus* in Umbria (central Italy).

2003 **Torres** *et al*. The situation of FD in Spain. Confirmation that only FD-D is present.

2004 **Angelini** *et al*.: A phytoplasma identical to FD-C isolate is found in wild Clematis in the vicinity of a FD-C affected vineyard in Veneto (Italy).

2004 **Lessio and Alma**: Study of the distribution of *S. titanus* within a vineyard and use of chromatic sticky traps. Abundance is greater in normal- than in low-density planted vineyards. *S. titanus* is monophagous. Leafhoppers are not able to spread significantly outside a vineyard. Females are less likely to fly far away than males.

B. BOIS NOIR (VERGILBUNGSKRANKHEIT, LEGNO NERO)

1. Description

Bois noir (BN) and related diseases are Grapevine yellows (GY) known in Europe and Asia Minor. The first observations in Eastern France date back to the early 1940's. BN was formally described in 1961 in comparison with Flavescence dorée (FD), because symptoms were similar. It was assumed that the two diseases were different because BN occurred in regions where the vector of FD was not present and experimental transmission with *S. titanus* was not successful. Because the vector insect, *Hyalesthes obsoletus*, does not live on vines, affected plants are usually not grouped into patches as with FD, except for situations where a high percentage of affected plants is observed. Nevertheless, distribution is non-random and spread follows a main direction or is preferentially along the border of the plot. BN has been identified in all wine-growing regions of western and eastern Europe, in Israel, Lebanon and recently in the Ukraine.

Main synonyms: The syndrome named Vergilbungskrankheit (VK) (1971) or Schwarzholzkrankheit (SHK) (2003) in Germany, Legno nero (LN) in Italy, Bois noir in Spain, has been occasionally described under the name of Flavescence dorée-like disease. Moreover, it has been sometimes confused with FD in the 1970's and 1980's. It is only since the 1990's that the aetiology was established and that it was shown that the agents of these diseases in the different countries were similar or closely related. Furthermore, the same vector insect species, *H. obsoletus,* has been identified in all countries, except for Spain where it appears to be very rare.

Main symptoms: All the main symptoms typical of GY can be found in BN / VK / LN - infected grapevines. In addition to leaf discoloration, growth abnormalities can be observed on canes and roots. Usually, only a few canes per plant show typical symptoms with either an uneven or a total lack of lignification. On white-berried varieties, yellow banding develops along the veins which may undergo necrosis. On red-berried varieties, sectorial reddening of blades develops in summer and progressively invades the whole leaf. When berries develop they remain immature, greenish and eventually fall down. Remaining berries are tasteless and sour. Internodes often show longitudinal rows of brown pustules along the green bark of unripe wood. Severely affected vines decline and may die after a few years. Some vines may recover or express irregular symptoms in successive years.

Agents: The phytoplasmas associated to these diseases belong to the stolbur group (16SrXII), a group that was for some time considered by some to be the I-G subgroup of the larger Aster yellows group (16SrI). Although stolbur phytoplasmas are ubiquitous pathogens, known to infect solanaceous crops as well as many weeds and bushes, only a limited number of strains have been identified. Hence the different names of BN disease appear to be more geographically than genetically significant.

Transmission: Vergilbungskrankheit (= Schwarzholzkrankheit) was the first disease for which the vector was identified. The known vector insect of stolbur of tomato, *H. obsoletus* (Homoptera, Cixiidae) can transmit stolbur phytoplasma to grapevine, but this occurs during feed probing as the insect does not keep feeding on grapevine. Hence, vine-to-vine transmission does not occur. The role of *H. obsoletus* has been confirmed in France, in Italy and Israel. In Spain, where the species is rare, its role in BN epidemiology must be verified. Alternative vectors have been suspected but not demonstrated. *H. obsoletus* is a univoltine polyphagous species that overwinters as larval instars that live on the roots of host plants. Nymph emerge in spring and transmission occurs during adult mating flights. Overall, the presence of insects on vines may last a couple of months. Eggs are laid during summer on the ground at the base of the stem of host plants. Main host plants of the insect vector are common weeds such as *Convolvulus arvensis*, *Ranunculus* sp., *Urtica dioica, Cardaria draba* and *Calystegia sepium.* However, only *C. arvensis* and *U. dioica* were found consistently infected with stolbur phytoplasma, distinct isolates of which were identified in these hosts. From 10 to 80% of trapped populations of the vector may test positive for the presence of stolbur phytoplasma.

Transmission by grafting is possible but only at a low rate. Since acquisition by the vector from infected vines does not seem possible, the significance of graft transmission on the spread of the disease is probably very low.

Varietal susceptibility and sensitivity: In the different affected regions and countries, numerous cultivars of *V. vinifera* were found susceptible to the stolbur phytoplasma, cv Chardonnay being the most sensitive. The increasing incidence of BN has been related to the increase of surfaces planted with Chardonnay in the last decade in all countries. Infection of rootstock varieties has not been reported. In all varieties there is a proportion of affected grapevines that undergo transitory recovery or remission, while other plants in the same plot are tolerant or immune to infection.

Other host plants: Stolbur phytoplasma is widespread, and has a wide host range. In addition to *C. arvensis*, *U. dioica, Ranunculus* sp., *C. draba* and *C. sepium,* shrubs and trees of *Prunus* spp., solanaceaous crops (tomato, tobacco, pepper, egg plant) and lavender (*Lavandula* spp.) may be significant reservoirs.

Detection: The use of monoclonal antibodies raised to stolbur phytoplasma did not show enough sensitivity for routine ELISA detection in field-grown infected grapevines. Detection is achieved mainly with PCR assays or PCR-RFLP analyses of DNA from infected host plants and insect vectors. Most often, nested PCR is necessary for sensitive detection from infected grapevines. Universal primers were first used to detect both BN and FD in areas where the two diseases may coexist. Subsequent RFLP analyses of amplified phytoplasma rDNA permit the characterization of pathogens. Stolbur specific primers have also been designed, either on variable regions of the rRNA gene or on selected specific non-ribosomal

DNA fragments. Combination of RFLP profiles of two DNA fragments allow the identification of three types of stolbur phytoplasmas associated to VK in Germany and hosted by different weeds. For direct differentiation between FD and BN/VK phytoplasmas, the multiplex nested-PCR assay cited in the FD chapter can be used.

Control: As with other GY diseases, no direct control is possible. Chemical sprays against *H. obsoletus* are not efficient, because of the complex biological cycle and multiple host plants of the insect species. Superficial soil cultivation in summer or winter ploughing are methods intended to damage the larval instars and reduce vector populations. Natural enemies are being investigated.

Recovery and remission of symptoms for several consecutive years are frequent in vines affected by BN. Hence, roguing should be avoided, except for declining vines. Though pruning does not cure infected vines, suppression of affected branches may improve harvest quality and help in progressive recovery.

2. Historical review

1961 **Caudwell**: Study on BN and its relationships to FD. BN is considered as a non epidemic form of FD.

1965 **Gärtel**: Description of VK under the name of Flavescence dorée. The disease occurs in the Moselle valley and the Rhine valley.

1968 **Leclant**: Presence of *Hyalesthes obsoletus* a cixiid planthopper in the south of France. The species has been described as the vector of stolbur "virus" by Suchov in USSR in 1948.

1969 **Leclant and Lacote**: Study of the ability to transmit stolbur to herbaceous plants by *H. obsoletus* in the south of France.

1971 **Caudwell** *et al*. (b): BN is distinct from FD based on non transmissibility by *S. littoralis,* absence of recovery, and different susceptibility and sensitivity of grapevine cultivars.

1971 **Mendgen**: 1971. Description of symptoms of VK, history, cytological and electron microscope study of tissues of affected grapevine. Description of structures that were probably closteroviruses, unknown at that time.

1972 **Caudwell** *et al*. (b): Epidemiological observations of BN lead to the assumption that an aerial vector is involved. Some grapevines show symptoms repeatedly in successive years, while others seem more tolerant and do not show symptoms.

1977 **Rumbos** *et al*.: Rickettsia-like organisms detected in phloem and xylem of roots of grapevines affected with VK in West Germany and in nematodes of the species *Xiphinema index* feeding on roots of these grapevines.

1978 **Nienhaus** *et al*.: Rickettsia-like organisms from VK-affected grapevines are cultured in chick embryos. Findings never confirmed.

1978 **Rumbos** *et al*.: Rickettsia-like organisms found in roots of VK-affected grapevines in the Saar, Mosel and Rhine valleys are considered as the causal agents of the disease and it is hypothesized that the nematode *Xiphinema index* is the vector of the disease. These findings have never been confirmed.

1988 **Credi and Callegari**: Survey of vineyards in Emilia-Romagna, Italy, for the presence of a FD-like disease. The results suggest that the disease is brought into the vineyards from outside local sources.

1989 **Borgo**: General information on the presence of FD-type diseases in northern Italy. *S. titanus* is not always associated with the disease.

1992 **Cazelles** *et al*.: GY symptoms are present in Switzerland (Suisse romande and Ticino) but they are not associated with *S. titanus*.

1992 **Fos** *et al*.: A monoclonal antibody raised to stolbur mycoplasma-like organism is used for ELISA detection of the agent in herbaceous host plants and insects. *H. obsoletus* is confirmed as a vector of stolbur disease plants in France.

1993 **Bertaccini** *et al*. (b): Evidence of an association of MLOs with grapevine yellows in Emilia-Romagna, Italy. The MLO strains found in grapevine are related with aster yellows MLOs, but are different from known strains of MLOs of the aster yellows cluster.

1993 **Bianco** *et al*. (a): Differentiation by PCR-RFLP of a MLO related to aster yellows in GY-diseased plants from Lombardia and a MLO related to elm yellows in an affected grapevine in Friuli-Venezia Giulia (Italy).

1993 **Cazelles and Kuszala**: Negative results with FD-ELISA on all tested GY-affected plants from Switzerland suggest that the GY present is BN rather than FD.

1993 **Daire** *et al*. (a and b): PCR-RFLP analysis of 16Sr DNA of MLOs show that the MLO associated with BN is different from the FD MLO and similar to the MLO associated with stolbur disease. BN MLO is detected in grapevines from France, from several regions of Italy, and from Israel.

1993 **Davis and Prince**: According to a different terminology, MLO associated to GY in Italy are related to aster yellows MLO.

1993 **Davis** *et al*. (a and b): PCR amplification of MLO DNA shows that MLOs associated with GY in several regions of northern Italy are related to the Italian periwinkle virescence (IPVR) MLO. The latter MLO was shown later to belong to the stolbur group.

1993 **Maixner** (b, c and d) Transmission of a yellows to periwinkle with dodder in Germany. It is suggested that vectors with preference for other host plants act as vectors for VK. Computer analysis for spatial patterns of spread shows a non-random distribution and suggests preferential transmission from other vines or from weeds.

1994 **Maixner** : Demonstration that *H. obsoletus* is a vector of VK in Germany.

1994 **Maixner** *et al*.: PCR-RFLP analysis of MLO-DNA detected in VK-affected grapevines in Germany show that this MLO is related to stolbur.

1994 **Minucci** *et al*.: The agent of a GY disease in the Italian Riviera is detected with a probe specific for Eastern aster yellows. PCR-RFLP analysis confirms relationship to aster yellows phytoplasmas.

1995 **Bertaccini** *et al*.: One of the two phytoplasmas detected in yellows-diseased grapevines in Liguria is related to IPVR phytoplasma, clustered by the authors into aster yellows group but shown later to belong to the stolbur group.

1995 **Laviña** *et al*.: First detection of BN (stolbur phytoplasma) in Spain.

1995 **Maixner** *et al*. (a): Development of stolbur-specific primers on phytoplasma rDNA and use for detection of stolbur phytoplasma in grapevines affected with VK and in the vector *H. obsoletus*. Several weeds are host plants of the stolbur phytoplasma.

1996 **Alma** *et al*.: Grapevines from Piemonte (northern Italy) contain several different phytoplasmas, the most frequent belonging to group 16SrI, subgroup I-G (later renamed as 16SrXII or stolbur group).

1996 **Bianco** *et al*. (b): Presence of phytoplasmas in the group 16SrI, subgroup I-G (later named group 16SrXII (stolbur) in the provinces of Vicenza, Brescia and Pavia (northern Italy).

1996 **Borgo**: Presence of BN in mixed infections with FD in the province of Treviso (Veneto, Italy) where FD is prevalent.

1996 **Boudon-Padieu** (b): History, aetiology and transmission of BN in France. *H. obsoletus* identified as the vector. Biology of the insect. Reservoirs and possible role of other vectors remain to be elucidated.

1996 **Koruza**: Survey of GY in three regions of Slovenia shows that the disease is of BN type. Estimated crop damage ranges from 20 to 40 %.

1996 **Kuszala**: Detection in ELISA using a monoclonal antibody to stolbur phytoplasma of BN-associated antigens in diseased grapevines in France. First detection of BN agent in diseased grapevines in Switzerland with the same procedure.

1996 **Maixner**: The situation of VK in Germany: symptoms, vector transmission and possible control measures.

1996 **Marcone** *et al*.: Phytoplasmas associated to GY in Campania (southern Italy) are genetically uniform and belong to the stolbur group, as well as phytoplasmas transmitted by Credi to periwinkle in Emila Romagna and previously classified in the aster yellows group.

1996 **Weber**: PhD thesis on the biology of the cixiid *H. obsoletus* and its role as the vector of VK.

1997 **Albanese** *et al*.: Important spread of GY symptoms on several grapevine varieties in Umbria (central Italy). Characterization of a phytoplasma belonging to group 16SrI, subgroup I-G (identified later as belonging to the stolbur group or 16SrXII).

1997 **Daire** *et al*. (a and b)*:* The identification with PCR-RFLP of rDNA of phytoplasma detected in European and Israeli grapevines affected by GY has shown that BN occurs in all regions. Search for variability among BN phytoplasmas with RFLP analysis of the specific non ribosomal DNA was unsuccessful.

1997 **Davis** *et al*. (c): Identification of stolbur phytoplasma (16SrXII) as agents of GYs in Greece and Israel.

1997 **Kölber** *et al*.: Occurrence of GY diseases in Hungary and identification of stolbur phytoplasma in affected grapevines.

1997 **Laviña** *et al*.: Prevalence of BN (stolbur phytoplasma) in Navarra and Cataluña (north eastern Spain). Preferential spread along the rows.

1997 **Maixner and Reinert** (a): Trials on elimination of VK infection from vine wood in Germany, using hot water treatment with conditions recommended in France. Results were satisfactory.

1997 **Maixner and Reinert** (b): Spatio-temporal analysis of the distribution of VK in 4 vineyards in the Moselle an Rhine valleys over a 2-3 year period showed a high incidence, a strong annual increase, a high proportion of previously infected vines that did not show symptoms for 2 years at least and, conversely, a high proportion of vines in which symptoms re-occurred after one season or more.

1997 **Osler** *et al*. (a and b): BN is poorly transmitted by bench-grafting. The maximum delay of symptom expression in young plants is 2 years.

1997 **Vindimian**: LN but not FD is present in Trentino (northern Italy) in spite of the presence and active spread of *S. titanus*.

1997 **Weber** *et al*.: Monitoring of field populations of *H. obsoletus* in Germany.

1998 **Maixner and Reinert**: A review of the research and present knowledge on VK and other GY diseases.

1998 **Refatti** *et al*.: Consistent association of stolbur phytoplasma with GY diseases in the Italian provinces of Fiuli-Venezia Giulia and Trento and in Slovenia.

1998 **Sforza**: PhD thesis on the epidemiology of BN in France, search for vectors, biology of *H. obsoletus* and possible control measures. Ploughing in winter of soils infested by *C. arvensis* is recommended to expose instar larvae and kill them with frost.

1998 **Sforza and Boudon-Padieu**: Description of *H. obsoletus* as a vector of BN.

1998 **Sforza and Bourgoin**: Anatomy of reproductory organs and mating of *H. obsoletus*.

1998 **Sforza** *et al*.: Epidemiology of BN in France. Confirmation of the role of *H. obsoletus* as a vector to grapevine. Acquisition may occur at larval stages since emerging 5th instars were infective. Identification of main reservoir weeds, among which hoary cress, formerly reported in western Europe.

1998 **Škoric** *et al*.: First detection of stolbur phytoplasma in grapevines in Croatia. Identification of two infected symptomless weeds in the vineyard.

1998 **Weber and Maixner** (a): Procedures for the survey of infection status of populations of *H. obsoletus* related to VK infection. Up to 34% of insects were infected with stolbur phytoplasma. PCR detection is reliable when testing together 25 insects among which only one is infected. Females are more often infected than males.

1998 **Weber and Maixner** (b): Ethololgy of *H. obsoletus* and possibility to control the insect in vineyards.

1999 **Seljak and Petrovic**: A review of the Slovenian situation of GY diseases. High rate of BN / LN infection in the different vine-growing regions**.**

1999 **Sforza** *et al*.: Ethological onservations and morphological descriptions of adults and larvae of *H. obsoletus*. First launching of colonies of the insect under controlled conditions.

2000 **Bourquin** *et al*.: Use of PCR to confirm the presence of stolbur phytoplasma in GY-affected grapevines in Switzerland.

2000 **Braccini and Pavan**: Report of survey of Auchenorrynchas in vineyards of Toscana (central Italy). *H. obsoletus* and *Metcalfa pruinosa* were found positive for BN phytoplasma (16SrXII-A).

2000 **Braccini** *et al*.: Widespread presence of LN in Toscana (central Italy). No other grapevine phytoplasma was detected.

2000 **Darimont and Maixner**: Comparison of the transmission efficiency of phytoplasma to their host plants and to grapevine by *H. obsoletus* and *Oncopsis alni*, the vector of Palatinate grapevine yellows (PGY), the second GY disease in Germany. The rate of infected *H. obsoletus* can be high because of the presence of reservoir weeds in the vineyard. Transmission to natural host plants is higher than for grapevine with both insects.

2000 **Larrue** *et al*.: Several vineyards affected by BN in Burgundy (France) monitored for over 15 years and assessed for symptom severity. Evidence secured for the occurrence of tolerance (no symptom at all for 15 years) and temporary remission (no symptoms for a few years) .

2000 **Maixner and Reinert**: Collection of *H. obsoletus* in vineyards is efficient with sticky traps placed at the soil level. Up to 30 % of the insects were infected and the highest rate was in vineyards with high populations of *Convolvulus arvensis.*

2000 **Maixner** *et al*.: VK disease dramatically increased in incidence in the Moselle and Rhine valleys during the 1990's. The study confirms a high rate of infected *H. obsoletus,* the ability to recover of cvs Riesling and Pinot in spite of systemic symptoms, and a high proportion of vines that escaped infection during the 3-5 year period of monitoring.

2000 **Marcone** *et al*.: Only stolbur phytoplasma detected in grapevines showing GY symptoms, regardless of the cultivar in Campania (southern Italy). The same pathogen detected in weeds and other crops.

2000 **Šeruga** *et al*.: BN reported only in north-western and eastern vineyards of Croatia. No other phytoplasma found in the South of the country.

2000 **Varga** *et al*.: In a large survey of vineyards in 8 Hungarian counties conducted in 1998, different phytoplasmas were identified in a number of cultivars. Phytoplasmas in the 16SrXII group (stolbur) were the most frequent.

2001 **Bertamini and Nedunchezhian**: Evaluation of effects of BN disease (stolbur phytoplasma) in field-grown grapevines, on pigments, chlorophyll fluorescence and photosynthetic activities suggest that Photo System II is affected. The authors conclude that phytoplasma infection induces non specific, general stress responses and rapid senescence**.**

2001 **Curkovic Perica** *et al*.: The situation of GY diseases in Croatia shows that only BN is present in the northern and eastern vineyards.

2001 **Darimont and Maixner**: Importance of the presence and infectivity of *H. obsoletus* to the German viticulture.

2001 **Gatineau** *et al*.: Anoder cixiid planthopper, *Pentastiridius* sp. is a natural vector of stolbur phytoplasma to sugarbeet in Bourgogne (France).

2002 **Alma** *et al*.: Demonstration that *H. obsoletus* is the vector of LN in Italy. Role of stinging nettle (*U. dioica*) as a reservoir of stolbur phytoplasma and as a host for the insect.

2002 **Gugerli** *et al*.: Only BN identified in Switzerland on cvs Chardonnay, Merlot and Pinot noir.

2002 **Maixner** *et al*.: The highest risk of phytoplasma contamination for grapevines coincides with the flight activity of adults of *H. obsoletus*. Indicators based on climatic parameters permit to predict the flight period.

2003 **Bertaccini** *et al*.: Importance of outbreaks of BN in the province of Modena (Italy) and monitoring of potential insect vectors in addition to *H. obsoletus*, which is widespread in the province.

2003 **Choueiri** *et al*.: Incidence of BN in a small area of the Bekaa valley (Lebanon) on cvs Chardonnay and Alicante Bouschet. All affected grapevines and two naturally infected periwinkles contained the same stolbur isolate, very similar to European isolates. The presence of *H. obsoletus* in Lebanon is recorded.

2003 **Cicotti** *et al*.: Observation of the occurrence of BN in Trentino in eight Chardonnay vineyards on more than 11,000 plants over 12 years. Same conclusions about tolerance and transient recovery of grapevines, reached by other authors.

2003 **Kölber** *et al*.: Survey of GY from 1997 to 2002 on 21 cultivars in 12 Hungarian counties. BN is the main disease and cvs Chardonnay and Zweigelt appear to be the more sensitive among white- and red-berried varieties, respectively. Severity of symptoms vary from one year to the other.

2003 **Langer** *et al*.: Comparison of infection risk by VK in organic and conventional vineyards in Germany. In spite of a similar abundance of *H. obsoletus* and the presence in organic vineyards of several weeds known as host plants carrying larvae on the roots, the incidence of VK was significantly higher in conventional vineyards. Attempt to bring up the larvae to the surface of the soil by ploughing so that they are killed by frost in winter is under evaluation.

2003 **Laviña** *et al*.: Assessment of the best period for detection of BN in affected grapevines. Samples were taken on all organs of 10 affected grapevines, every month for one year except in winter. Detection in December was the more constant.

2003 **Mescalchin and Mattedi**: A description of the development of VK in Trentino (northern Italy)**.**

2003 **Morandell**: Detection of VK in south Austria.

2003 **Myrta** *et al*.: First detection in Albania of BN phytoplasma in grapevines of different age and varieties.

2003 **Orenstein** *et al*.: Survey of potential vectors of phytoplasmas in vineyards of the Golan Heights. *Neoaliturus fenestratus*, *H. obsoletus* and *Circulifer haematoceps* were widespread and positive for stolbur or aster yellows phytoplasmas, while *Megophthalmus scabripennis* was positive for aster yellows phytoplasma. Study of the spatial and temporal dispersion of the four species.

2003 **Petrovic** *et al*.: Importance of a GY epidemics in the Drava region (Slovenia) in 2001 and 2002, together with high populations of *H. obsoletus* and frequence of *C. arvensis* and *U. dioica*.

2003 **Sabaté** *et al*.: Search for vectors of stolbur phytoplasma in Cataluña (Spain) where *H. obsoletus* is rare. Trapping of insects on sticky traps or with D-Vac suction. Living insects checked for transmissibility of phytoplasma by feeding on artificial medium. Several hemipters have been found to deliver stolbur phytoplasma to the medium. Transmission to plants is not reported.

2003 **Šeruga** *et al*. (a): Investigation on the variability of stolbur (16SrXII) phytoplasmas from extracts of different grapevines in Croatia, using 4 fragments of phytoplasma DNA showed that all isolates are similar.

2003 **Šeruga** *et al*. (b): First identification of BN infection in the Macedonian republic.

2004 **Gilge** *et al*.: Important epidemics of "Schwarzholzkrankheit" (SHK = VK) in Franken (Bayern, Germany). Symptoms were recorded on 26% of 30-year old Scheurebe grapevines and 96% of tested individuals of *H. obsoletus* were positive for stolbur phytoplasma.

2004 **Langer and Maixner**: Three different types of stolbur phytoplasma isolates found in grapevines, *H. obsoletus* and weeds in different areas in Germany. According to the data of field survey, specific association of each isolate with a different weed is discussed.

2004 **Milkus** *et al*.: Important expression of BN in cv Chardonnay in the Ukraine.

C. PALATINATE GRAPEVINE YELLOWS

1. Description

Palatinate grapevine yellows (PGY) is a disease occurring in Germany in Pfalz and Moselle regions (west of Germany) mainly on cv Scheurebe. The disease was identified in 1995. It is associated to phytoplasmas in the Elm yellows (16SrV) group. It is not epidemic and occurs most often in old vines in vineyards along creeks or rivers where alders (*Alnus glutinosa* L) are present.

Main synonyms: FD-Pfalz was a first name because the agent was shown to be related to the FD phytoplasma.

Main symptoms: Symptoms are similar to those of other GY diseases and may affect the whole plant. However, affected plants are not numerous, occur most often at the border of plots, and rarely in groups.

Agents: The agent is an EY (16SrV) group phytoplasma. Three isolates (PGY-A, -B and C) have been identified. PGY phytoplasma is similar to the Alder yellows phytoplasma that is widespread in black alder in Germany. It is different from FD phytoplasma. Alder is considered as the source of PGY infection.

Transmission: Transmission was obtained with the leafhopper *Oncopsis alni* Schrank (Hemiptera, Cicadellidae) trapped on alders and caged on *V. vinifera* seedlings that later developed GY symptoms. *O. alni* is highly monophagous and specimen do not survive long on grapevine. Another alder insect, the psyllid *Psylla alni*, was found carrying the alder phytoplasma at a higher rate than *O. alni* but failed to transmit both to alder and grapevine. Attempts to transmit PGY phytoplasma from grapevine to grapevine using reared *S. titanus* leafhoppers have failed. The latter results have not been published.

Varietal susceptibility and sensitivity: PGY occurs in limited areas, mainly on cv Scheurebe.

Other host plants: Alder trees (*Alnus glutinosa* L.)

Detection: Universal primers and RFLP analysis of amplicons can be used to identify a 16SrV phytoplasma. More specific characterization can be obtained with EY-group specific primers fAY/rEY that amplify a 16S rDNA fragment or with FD9 primers that amplifiy the non ribosomal FD9 DNA fragment. RFLP of FD9 fragment permit to distinguish PGY phytoplasmas from FD phytoplasmas and from other phytoplasmas in the same group (see the Flavescence dorée chapter).

Control: No possibility of control because of erratic transmission by the vector.

2. Historical review

1995 **Maixner** *et al*. (b): Detection of a new EY-related phytoplasma in GY-affected cv Scheurebe in Germany. It is different from FD phytoplasma but molecular and serological data show a close relationship.

1997 **Reinert and Maixner**: 1997. Identification of the PGY-associated phytoplasma with phytoplasmas infecting alder in the vicinity of affected vineyards. Same RFLP profiles of P1-P7 rDNA amplicons obtained from yellows affected grapevines, alder, *Oncopsis alni* and *Psylla alni* specimen, both insect species trapped on alder.

1999 **Maixner and Reinert**: Demonstration that *O. alni* (Auchenorrhyncha, Cicadellidae) (but not *P. alni*) is able to transmit the alder yellows phytoplasma to healthy seedlings of alder. The alder phytoplasma resembles ALY, a phytoplasma isolate transmitted from alder to periwinkle in Italy.

1999 **Reinert**: PhD thesis on detection, molecular characterisation and epidemiology of PGY. Variability analysis and sequencing of the FD9 DNA fragment and homology of the sequence to a part of the *SecY* gene.

2000 **Darimont and Maixner**: Comparison of the transmission efficiency of phytoplasma to their host plants and to grapevine by *O. alni* and *H. obsoletus*, the vector of BN / VK. The proportion of infective leafhoppers is lower with *O. alni*. The risk of infection by PGY is lower than for VK because reservoir plants are fewer and outside vineyards.

2000 **Maixner** *et al*. (b): Transmission to *V. vinifera* seedlings of the PGY phytoplasma using specimen of *O. alni* trapped on alders. The strong adaptation of *O. alni* to alder prevents a frequent inoculation to grapevine even if the infestation of the leafhopper population is high. As much as 5 % of leafhoppers from Palatinate and 15 % from Moselle tested positive.

2000 **Reinert and Maixner**: All the 3 strains of PGY were detected both in alder trees and in specimen of *O. alni*. Characterization of the three PGY strains showed that they were closer to FD than to strain EY1 from American elm. Extensive survey of yellows-affected grapevines in several areas of Germany did not show the presence of other EY group phytoplasmas.

2001 **Angelini** *et al*.: Comparison between Elm yellows group (16SrV) phytoplasmas including PGY strains, 4 Italian and French strains of FD and elm and alder phytoplasmas. The PGY strains are closest to the ALY phytoplasma from alder in Italy and to one strain of FD.

2003 **Angelini** *et al*.: Further comparison between elm yellows group (16SrV) phytoplasmas, using Heteroduplex mobility assay and sequencing of rDNA and FD9 fragment. The differences in vector specificity between PGY and FD phytoplasmas are not supported by molecular data.

D. NORTH AMERICAN GRAPEVINE YELLOWS

1. Description

Grapevine yellows (GY) were first reported in New York State (USA) in 1977. In 1991, populations of *S. titanus* living mostly on wild *Vitis riparia* around affected vineyards were found to carry an agent that was serologically related to that of FD. However, the latter findings were not confirmed. In 1993, a phytoplasma belonging to the X-disease group (16SrIII) was detected in affected grapevines in New York. In the same period, a serious outbreak of GY occurred in Virginia, which was associated with two different phytoplasmas in group 16SrIII and 16SrI (aster yellows), respectively.

Main synonyms: Leaf curl and berry shrivel (LCBS), American grapevine yellows.

Main diseases: Virginia grapevine yellows I (VGYI), Virginia grapevine yellows III (VGYIII)

Main symptoms: North American Grapevine Yellows (NAGY) is a lethal disease causing yellowing of the leaves, die back of shoot tips and abortion of developing fruit. Infected grapevines often die within months from the onset of symptoms and significant losses of vines have been observed. In New York, affected vines often do not survive winter frost because they lack reserves.

Agents: The 16SrIII phytoplasma detected in NY has not been further characterized. The Virginia Grapevine Yellows (VGY) has been associated with the VGYIII phytoplasma (a strain of X-disease or 16SrIII, subgroup III-B) and with the VGYI phytoplasma (a strain of aster yellows or 16SrI, subgroup I-A).

Transmission: No vector insects have been identified for VGY phytoplasmas. However, the survey of vineyards and transmission assays to *V. vinifera* cuttings, faba bean plants and feeding solutions, as well as direct PCR assays from insects, allowed the identification of a few candidate vectors of the aster yellows phytoplasma, among which *Agallia constricta*. X-disease phytoplasma was detected in native *Vitis* sp. and aster yellows was detected from numerous weeds and shrubs within and around the vineyard. No transmission by vine planting material reported.

Varietal susceptibility and sensitivity: In New York, the disease was first observed on cv De Chaunac, then on White Riesling. In Virginia, it is very severe on Chardonnay vines but was observed on other varieties including Riesling, Sauvignon blanc and Cabernet franc.

Other host plants: Both phytoplasmas are widespread in the USA in weeds and cultivated species. X-disease phytoplasma was detected in native *Vitis* sp. and an aster yellows phytoplasma was detected in numerous weeds and shrubs within and around the vineyards.

Detection: With molecular assays using universal or group-specific PCR primers. The X-disease phytoplasma occurring in New York was also detected with monoclonal antibodies and with probes for dot-blot hybridization.

Control: There are no control methods since vectors and reservoirs of the associated phytoplasmas are still undetermined.

2. Historical review

1977 **Uyemoto** *et al*.: Description of a disease of the yellows type affecting the variety De Chaunac in vineyards of New York State denoted Leaf curl and berry shrivel (LCBS). It appeared to be spreading and was perhaps insect borne.

1985 **Pearson** *et al*.: Occurrence of FD-like symptoms on White Riesling grapevines in New York. Symptoms, very similar to those of LCBS, observed in 1983. Symptoms may occur for several years in succession in the same vines.

1991 **Maixner and Pearson**: First data on the study on *S. titanus*, present in New York and its possible relationship with a GY disease.

1993 **Chen** *et al*.: Two MLOs were transmitted from affected grapevines to periwinkles in Udine (Italy) (= FDI or FDU or GYU) and New York. Extracts of periwinkles were used to raise two monoclonal antibodies and to design oligonucletides that were used as probes in DNA-DNA hybridisation or as PCR primers. ELISA and immunfluorescence were positive from periwinkle. Probes and primers yielded positive reactions using DNA extracted from grapevine. Data showed that the Italian and American MLO were related. Detection was positive in symptomless wild *Vitis riparia* growing near vineyards in New York and in some symptomatic grapevines. However, other grapevines with strong symptoms tested negative. The latter observation suggests that another non-related MLO might have been present. The FDI MLO was identified in a parallel work as a member of the X-disease group.

1993 **Daire** *et al*. (a): A Riesling plant from New York and a periwinkle carrying the FDI MLO described above, tested positive for a MLO in the X-disease group with PCR-RFLP of 16S rDNA.

1993 **Maixner** *et al*.: Monitoring of *S. titanus* in New York and transmission assays of a possible infectious agent. Larvae are more frequent on wild *Vitis riparia* at the border of the vineyards. Adults migrate from *V. riparia* to *V. vinifera*.

1993 **Prince** *et al*.: Molecular comparisons between MLOs transmitted to periwinkle from grapevine or detected in a few naturally affected grapevines, show that the FDU (= FDI) strain from Italy and a MLO detected in a grapevine in Virginia (USA) are both related to X-disease.

1993 **Wolf** *et al*.: A GY disease observed in Virginia since 1983 affects large areas with a low incidence and a low spread rate. The relatedness of the associated MLO to X-disease MLO is confirmed.

1998 **Davis** *et al*.: Two phytoplasmas are detected in yellows diseased grapevines in Virginia. Confirmation that a X-disease (16SrIII) group phytoplasma is involved and classification of the latter phytoplasma into a new subgroup, III-I. The second phytoplasma, also detected in wild *V. riparia* vines, is a member of the aster yellows (16SrI) group, subgroup I-A.

2003 **Beanland and Wolf**: Search for possible insect vectors and reservoirs of NAGY phytoplasmas in Virginia. *Agallia constricta* is a suspected vector of VGYI (aster yellows phytoplasma). Other species tested positive and transmitted to feeding solutions. Both VGYI and VGYIII were found in several weeds and shrubs around and inside the vineyards.

E. AUSTRALIAN GRAPEVINE YELLOWS

1. Description

Grapevine yellows were first reported from Australia in 1976 and called Australian grapevine yellows (AGY) in 1983. The association of AGY with phytoplasmas was confirmed as early as 1988. Early and recent surveys have shown that AGY are found in most viticultural regions of Australia, with a higher incidence in warmer inland districts of New South Wales and South Australia. The use of PCR has shown the association with AGY of three different phytoplasmas. In addition, two syndromes with particular symptoms (Restricted Growth and Late Season Leaf Curl) have been found in some cases, consistently associated with AGY symptoms and AGY phytoplasmas but their aetiology is not clear. Conversely, there are reported cases where they were not associated with AGY disease or phytoplasmas.

Main diseases: AGY (*sensu stricto*); Buckland Valley Grapevine Yellows (BVGY), a GY disease found in Victoria (Australia); Restricted Growth (RG), Late Season Leaf Curl (LSLC).

Main symptoms: All symptoms typical for GY can be found on AGY-diseased plants. Affected vines carry one or more shoots with irregular veinal of interveinal yellowing and downward rolling of the leaves that overlay one another in a shingled fashion. The yellow leaf tissue can become necrotic. Shoots may display abortion of bunches or berry shrivel later in the season and death of terminal buds, followed by the progressive death of the shoots, one node after the other. In this particular disease, leaves tend to fall early. Stems of affected shoots develop a blue, waxy appearance and remain rubbery. Mapping of diseased plants show that grapevines appear to be a terminal host of AGY, suggesting that the source is from an alternative host.

Restricted Growth (RG)-affected grapevines show retarded growth resulting in shortened shoots and smaller leaves. Some plants also display uneven bud development resulting in canes and cordons that are bare in places with little or no bunch development.

Late Season Leaf Curl (LSLC)-affected grapevines show symptoms in late summer with tightly downward rolled leaves that often remain green, overlay one another like shingles and become leathery and brittle.

Agents : AGY disease (*sensu stricto*) is associated with two phytoplasmas: the AGY phytoplasma, which is the more frequent and the Tomato big bud (TBB) phytoplasma. The AGY phytoplasma has been designated as *Candidatus* species "*Candidatus* Phytoplasma australiense". It belongs to the stolbur group (16SrXII) but is distinct from the BN and VK phytoplasmas. The 16S rRNA gene has a high sequence similarity (more than 99.5%) with the phytoplasmas associated to Papaya die back (PDB) in Australia and to *Phormium* yellow leaf (PYL) in New Zealand, respectively. It has been suggested that all three phytoplasmas are strains of the same phytoplasma species. The TBB phytoplasma has been designated as *Candidatus* species "*Candidatus* Phytoplasma australasia". It belongs to the peanut witches' broom group (16SrII) and has a broad plant host range in Australia.

BVGY phytoplasma has not been clustered in an established phytoplasma group. The sequence similarity of the 16S rRNA gene shows that it is close to members of the aster yellows group (16SrI), clover phyllody phytoplasma (16SrI-C) being the closest .

Transmission: No vectors have been identified for any AGY disease. The AGY phytoplasma was detected in the common leafhopper *Orosius argentatus* (Evans) but transmission to grapevine has not been reported. The planthopper *Oliarus atkinsoni* Myers (Hemiptera, Cixiidae) is known as the vector of PYL disease in New Zealand but the species has not been reported from Australia. The TBB phytoplasma is transmitted to other crops by *O. argentatus*. Recent studies have shown that the latter phytoplasma can be acquired from infected grapevine by *O. argentatus* and subsequently transmitted to faba bean but the ability to transmit to grapevine was not confirmed. The BVGY phytoplasma has no suspected insect vector. However, this phytoplasma is associated with GY disease in vineyards in the same restricted grape-growing areas that were established with planting material from different sources, suggesting that the disease is the result of an aerial transmission and that the phytoplasma was not present in the original planting material.

Varietal susceptibility and sensitivity: Chardonnay and Riesling appear to be most often affected, but phytoplasmas were also detected in other red- and white-berried varieties, such as Shiraz or Semillon. It is possible that AGY diseases have become prevalent in Australia in the last years with the increasing planting of Chardonnay.

Remission of AGY, RG and LSLC diseases has been observed. A "heat curing" effect of AGY disease by hot weather has been observed, suggesting that this contributes to the decline in phytoplasma numbers and to the remission of symptoms. However, once vines are infected by AGY, RG or LSLC, they are at greater risk of displaying symptoms again in the following years, indicating persistence of the disease.

Other host plants: As mentioned above, AGY phytoplasmas are common in several crops in Australia. Several observations suggest that aerial transmission prevails. Hence, reservoirs must be important but the epidemiology is not fully understood.

Detection: Detection is obtained with PCR. All generic "universal" primers may be used, followed by RFLP analysis or sequencing. Specific primers have been designed on the 16S rRNA gene for detection of AGY phytoplasma (*Ca*. Phytoplasma australiense) either in single-step or nested PCR following a first amplification with universal primers. Similarly, a specific primer in the intergenic 16S-23S spacer region has been designed for detection of TBB phytoplasma (*Ca*. Phytoplasma australasia). Detection can be from shoots, branches, trunks and roots throughout the year and infection is persistent from year to year. Sampling simultaneously from shoots, branches, and trunks in October is more reliable.

Control: There are no methods to control AGY diseases in the vineyard. Sanitation with hot water treatment is being developed in Australia.

2. Historical review

1982 **Magarey and Wachtel**: Description of a new disease of the yellows type in cv Rhine Riesling in South Australia.

1983 **Magarey** *et al*.: The "Rhine Riesling problem" denoted "Australian Grapevine Yellows".

1985 **Magarey and Wachtel**: Review of the AGY problem. Reduction of symptom expression in vines injected with tetracycline. Phloem fluorescence of diseased vines in the UV microscope.

1986 **Magarey**: Comprehensive review of GY diseases in the world.

1986 **Magarey and Wachtel**: GY symptoms are found in most viticultural areas of Australia. The incidence of disease may be temporarily high in some vineyards of Chardonnay.

1988 **Magarey**: The situation of GY in Australia.

1988 **Magarey** *et al*.: MLOs, 140-510 nm in diameter, found in sieve tubes of diseased vines are associated with AGY symptoms.

1989 **Osmelak** *et al*.: *Orosius argentatus*, vector of TBB in tomato crops, is found in high numbers together with two other potential MLO vectors in vineyards of Victoria (Australia).

1995 **Bonfiglioli** *et al*. (a and b): Positive detection of phytoplasma with PCR in AGY-affected grapevines and tentative survey of phytoplasmas in Australia.

1995 **Padovan** *et al*. (a and b): The phytoplasma associated with AGY is related to an aster yellows type phytoplasma associated with GY in Italy (later on identified as the stolbur phytoplasma).

1996 **Padovan** *et al*.: Further comparison of AGY phytoplasma with overseas GY phytoplasmas show that it is closely related to, but different from the stolbur phytoplasma associated with BN in France, Spain and Israel.

1997 **Bonfiglioli** *et al*.: Assumption from field observations and monitoring that AGY, RG and LSLC are associated. LSLC would be followed by AGY on the following year and AGY would be followed by RG in subsequent years.

1997 **Davis** *et al*.: Description of the AGY phytoplasma and designation of a new taxon, *Candidatus* Phytoplasma australiense.

1997 **Wilson** *et al*.: Description of AGY symptoms.

1998 **Constable** *et al*.: Detection of phytoplasmas associated with AGY, RG, and LSLC.

1998 **Kelly** *et al*.: No vector for AGY found. Hence, insecticide sprays are useless for controlling the disease.

1998 **Liefting** *et al*.: Close relationships between phytoplasmas associated with AGY, Papaya dieback and Phormium yellow leaf diseases.

1999 **Beanland** *et al*.: AGY phytoplasma detected in the body of *Orosius argentatus* leafhoppers.

1999 **Constable and Symons**: AGY phytoplasma is detected in most symptomatic grapevines but also TBB phytoplasma and a third uncharacterised phytoplasma, later called BVGY phytoplasma. Uneven distribution of phytoplasmas in infected plants. Spring and summer are optimal for detection.

1999 **Gibb** *et al*.: The AGY phytoplasma is consistently present in the majority of symptomatic grapevines. It is occasionnally detected in symptomless vines and in vines with LSLC or RG symptoms. The TBB phytoplasma is detected occasionnally in vines with AGY symptoms and also in LSLC-affected vines.

2000 **Constable** *et al*.: Identification of a new phytoplasma in Chardonnay grapevines in Victoria (Australia).

2000 **Habili** *et al*.: Comparison of visual assessment and diagnostic assays. The problem of symptomlessly infected vines.

2001 **Beanland** *et al*.: TBB phytoplasmas can be acquired from diseased grapevine by *Orosius argentatus* and subsequently transmitted to faba bean.

2001 **Waite** *et al*.: Use of hot water treatment in commercial nurseries of Australia.

2002 **Constable**: PhD thesis on the biology and epidemiology of AGY phytoplasmas.

2002 **Constable** *et al*.: Study of the phylogenetic relationships of the BVGY phytoplasma with aster yellows and stolbur phytoplasmas. BVGY might form a new AY subgroup of AY *(*16Sr*)* group or even a new phytoplasma group.

2002 **Constable** *et al*.: BVGY phytoplasma is associated to GY symptoms that may show remission then reoccurrence but also appear on vines that were not affected previously, resulting in increasing cumulative incidence. Detection of BVGY in another plot in the same area, established from a different source of plant material indicate that BVGY disease occurs as a result of aerial transmission.

2002 **Crocker** *et al*.: The management of the area for plant material in the nursery with the scope of hot water treatment.

2003 **Constable** *et al*. (a and b): Biology and epidemiology of AGYs. The AGY and the TBB phytoplasmas may persistently affect grapevines throughout the year and between years. Symptomatic shoots from AGY affected vines are reliable for detection in summer (January). At other times of the year, detection is more reliable from samples taken from branches and trunks.

2004 **Constable and Symons**: Study with Heteroduplex mobility assay (HMA) of the elongation factor Tu (*Tuf*) gene of the AGY and the BVGY phytoplasmas. Two isolates of AGY and Papaya dieback (PDB) phytoplasma did not show variability between them but showed some variability when compared to a reference AGY phytoplasma. No variability was observed amongst BVGY phytoplasma isolates.

2004 **Constable** *et al*.: Survey of AGY, RG and LSLC symptoms for 3 to 6 years in Chardonnay and Shiraz vineyards. In Chardonnay, the diseases are characterized by remission in some plants, recurrence in other vines and new occurrence in previously unaffected vines. The total cumulative incidence for AGY could be as high as 90%. Statistical analysis showed that RG and LSLC diseases were not always associated with AGY. However, TBB phytoplasma may have a role in the aetiology of LSLC. There is no information of transmission of AGY by planting material. The incidence of AGY in a plot of cv Shiraz that had been treated with hot water suggests that AGY phytoplasmas are introduced to vineyards by aerial transmission.

F. OTHER GRAPEVINE YELLOWS

1. Description

Besides the cases reported above, three different situations must be described. The first is the detection in countries other than the USA, of phytoplasmas belonging to the aster yellows group (16SrI) in yellows-affected grapevines, sometimes as a second phytoplasma in co-infection with FD or BN phytoplasmas and sometimes also in symptomless grapevines. These aster yellows phytoplasmas belong to subgroups I-B or I-C (clover phyllody) which are ubiquitous in Europe. They must not be confused with the 16SrI-G phytoplasma of earlier reports, which was the first designation for stolbur phytoplasma in some laboratories, later designated 16SrXII. It seems that aster yellows phytoplasmas have no important significance in European grapevine yellows. However, they seem to have some relevance in Israel and were recently reported from Tunisia. The second situation is the significant occurrence of X-disease group (16SrIII) phytoplasmas in countries other than the USA, namely Israel. The third situation is represented by poorly characterized GYs recorded from new countries.

Transmission: Aster yellows and, to a lesser extent, X-disease group phytoplasmas, are very frequent in many host plant species and several insect species are known as vectors or potential vectors in different countries.

Varietal susceptibility and sensitivity: Chardonnay, a variety widely grown in all countries and very sensitive to all GY agents, is often reported in connection with these cases. Other varieties are cited in the different situations.

2. Historical review

Europe

1996 **Alma** *et al*.: Survey of phytoplasmas infecting grapevine in northern Italy. In three instances, a 16SrI-B phytoplasma was found in mixed infection with a stolbur phytoplasma (at that time designated 16SrI-G).

1997 **Saric** *et al*.: Detection of phytoplasma in the aster yellows group in GY affected plants in Slovenia and Croatia. The subgroup of aster yellows was not determined but primers specific for stolbur tested negative.

2001 **Alma** *et al*.: Experimental transmission of the Chrysanthemum yellows phytoplasma (16SrI-B) to grapevine by four leafhopper species, including *S. titanus*. Similar transmission of clover phyllody (16SrI-C) MLO by *S. titanus* had been obtained in 1971 in France (cf. Caudwell *et al*. 1971b).

2003 **D'Ascenzo** *et al*.: A 16SrI-C phytoplasma was found associated with GY in relevant percentages in the same vineyards as stolbur (BN) phytoplasma in Abruzzo region (eastern central Italy).

Israel

1997 **Tanne and Orenstein**: Grapevine phytoplasmas in Israel were transmitted to periwinkle with heterografting and identified in the periwinkle as 16SrIII and 16SrI phytoplasmas.

2000 **Tanne** *et al*.: Monitoring of potential phytoplasma vectors in vineyards in Israel and molecular detection of phytoplasmas in their body. *Neoaliturus* sp*., Orosius orientalis*, *Macrosteles sexnotatus*, *Circulifer* spp. and *Anaceratagalia laevis* were all found carrying an aster yellows phytoplasma. In addition, a X-disease phytoplasma was detected in some *Neoaliturus* specimen.

2001 **Klein** *et al*.: Further survey of GY vectors in the Golan Heights. *H. obsoletus* was found in addition to the preceding 5 species.

2003 **Orenstein** *et al*.: Survey over several years of potential vectors of phytoplasmas in vineyards of the Golan Heights showed that *Neoaliturus fenestratus, H. obsoletus* and *Circulifer haematoceps* were all three abundant and positive for stolbur and aster yellows phytoplasmas. *Megophthalmus scabripennis* was positive for aster yellows phytoplasma. The spatial and temporal dispersion of the four species was analysed.

Tunisia

2003 **Chabbouh** *et al*.: First results on the monitoring of GY diseases in Tunisia in imported table grape varieties. Trapping of hemipters and identification of numerous potential phytoplasma vectors. Transmission to periwinkle of yellows diseases using collected insects. Detection with PCR show erratic identification of a 16SrI-B phytoplasma.

2003 **M'hirsi** *et al*.: Formal identification of a 16SrI-B phytoplasma in GY-affected grapevines in Tunisia.

South America

1980 **Caudwell**: Description of a disease of the yellows type in Chile, called "Amarilliamento de Elqui". In addition to similarities of symptoms with FD, some affected vines showed a sudden fall of leaves in summer.

2003 **Gajardo** *et al*.: Identification in yellows-affected vines of varieties Petit Syrah, Merlot and Carmenere, of phytoplasmas belonging to group 16SrI, subgroups I-B and I-C and also to group 16SrVIII (Ash yellows) in mixed infection with I-B. Stolbur phytoplasma (16SrXII) was also detected.

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