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Sources of resistance to grapevine fanleaf virus (GFV) in *Vitis* species

by

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Träger von Resistenzen gegen das Virus der Reisigkrankheit (grapevine fanleaf virus, GFV) bei *Vitis*-Arten

Zusammenfassung: Zur Ermittlung von Rebstämmen, die gegen das Virus der Reisigkrankheit (grapevine fanleaf virus, GFV) resistent sind, wurde ein breites Spektrum von *Vitis*-Genotypen getestet. Die 173 überprüften Reben umfaßten *Vitis*-Arten, Kultursorten und interspezifische Kreuzungen. Da angenommen wird, daß *V. vinifera* und das GFV einen gemeinsamen Ursprung im Mittleren Osten haben, wurde der Species *V. vinifera* besondere Aufmerksamkeit geschenkt; 27 *V.-vinifera*-Abkömmlinge aus dem Mittleren Osten und 9 Kultursorten von *V. vinifera* kamen in den Test. Zusätzlich wurden nordamerikanische Abkömmlinge von 24 *Euvitis*- und 2 *Muscadinia*-Arten einschließlich Kultursorten von *V. rotundifolia* sowie 5 asiatische Species überprüft. Zu den interspezifischen Hybriden zählten 3 *V. vinifera* × *V. rotundifolia*- (VR-)Kreuzungen, an denen sich der Nematode *Xiphinema index*, der Vektor des GFV, bekanntlich nicht ernähren kann. Die zu untersuchenden Reben wurden auf infizierte Cabernet-Sauvignon-Stöcke gepfropft und anschließend mittels ELISA auf die Anwesenheit des Virus geprüft. Es konnten 3 GFV-resistente Reben identifiziert werden — ein *V.-vinifera*-Abkömmling aus dem Mittleren Osten, die *V.-rotundifolia*-Sorte Bountiful und eine der VR-Hybriden. Mehrere *V.-vinifera*-Reben (einschließlich einiger Kultursorten), die früher als GFV-resistent galten, erwiesen sich in der vorliegenden Untersuchung als virusanfällig. Die Resultate deuten auf zwei Formen von GFV-Resistenz bei *Vitis*-Genotypen hin, eine „Wirtspflanzen-" und eine „Nichtwirts-Resistenz" (HEATH 1981).

Key words: fanleaf, virus, Vitis, variety of vine, transmission, serology, selection, resistance, gene resources.

Introduction

Infectious degeneration, caused by grapevine fanleaf virus (GFV), is a major disease throughout the world's viticultural areas. The virus is spread via both propagating materials and the nematode vector, *Xiphinema index.*

Since the identification of the nematode vector by HEWITT *et al.* (1958), there have been attempts to control this disease by exploiting its soil-borne nature. Clean stock programs utilizing heat therapy (GOHEEN and LUHN 1973; BOVEY 1980) have been effective in supplying virus-free propagating materials, but, if the nematode vector is present in the soil, reinfection of the replanted vineyard will occur. Attempts to limit or kill the vector with nematicides and fumigants have been ineffective in California's deep fertile soils (RASKI *et al.* 1983). A resistant rootstock might control this desease.

Resistance to *X. index* feeding has been identified in several *Vitis* species (KUNDE *et al.* 1968; BOUBALS and PISTRE 1977; BOUQUET 1980; WEISCHER 1980) and is now being exploited in rootstock breeding programs in France (BOUQUET and DANGLOT 1983) and California (LIDER, GOHEEN, RASKI, GRANETT, and MEREDITH, unpublished). However, nematode feeding resistance may not be enough to control this disease. ALFARO and GOHEEN (1974) have established the minimum acquisition threshold for transmission of

GFV from nematode to grapevine to be 5 min. Given this short acquisition time and the possibility that *X. index* could overcome feeding resistance, a rootstock which incorporates both feeding resistance and resistance to GFV is highly desirable. A prerequisite to such a breeding program is the identification of GFV-resistant germplasm. We report here the identification of several sources of GFV resistance as the result of an extensive screening of *Vitis* germplasm.

Material and methods

Germplasm surveyed

The germplasm screened in this survey is listed in Table 1. All the plant material was obtained from the vineyard of the Department of Viticulture and Enology, University of California, Davis, with the exceptions of *vinifera* # 26 and # 27 which were gifts from the private collection of H.P. Olmo and *rupestris* cv. St. George which was obtained from the Department of Plant Pathology, University of California, Davis.

Propagation

The accessions were propagated from both green shoots and dormant wood, as was the GFV-infected inoculum material. Rooted cuttings were grown in 10 cm plastic pots in steam-sterilized soil consisting of equal parts of sand, clay loam, fir mulch and vermiculite.

GFV source

The GFV inoculum was in the form of known infected *vinifera* cv. Cabernet Sauvignon cuttings from a Napa Valley, California, vineyard. All the cuttings were made from vines that expressed the vein-banding sympton of GFV. Infection in these vines was confirmed by enzyme-linked immunosorbent assay (ELISA).

Inoculation

The candidate vines were inoculated with a green wood tongued-approach graft (Hartman and Kester 1975) to GFV-infected Cabernet Sauvignon plants. This graft technique involves two independent self-sustaining plants, thus reducing grafting difficulties and increasing graft success. Green grafting has also been shown to overcome incompatibility between unrelated species of *Vitis* (Taylor *et al.* 1967; Bouquet and Hevin 1978).

Both candidate and inoculum plants were pruned back to 2-bud shoots 1 month prior to grafting to allow uniform green shoots to develop. 2 months after grafting all of the plants were pruned to 2 buds above the graft union to provide conditions favorable for virus replication.

The grafts were made in two groups. The first group of approximately half of the accessions was completed between July 6 and July 19, 1983 and the second group between August 29 and September 2, 1983. There were 4 grafted plants and 1 ungrafted control for each accession.

Greenhouse conditions

The plants were grown in a greenhouse between 15 and 27 °C. It was heavily whitewashed to moderate high summer temperatures and supplementary fluorescent

Table 1

Vitis germplasm surveyed for resistance to grapevine fanleaf virus

Auf ihre Resistenz gegen die Reisigkrankheit untersuchte *Vitis*-Genotypen

Species	Number of accessions tested
A. North American *Euvitis*	
aestivalis	3
arizonica	1
berlandieri	3
californica	1
candicans	3
champini	4
cinerea	9
cordifolia	10
doaniana	1
gigas	2
girdiana	1
labrusca	3
lincecumii	2
longii	10
monticola	10
palmata (rubra)	1
riparia	11
rufotomentosa	1
rupestris	
wild	6
cultivars	1
St. George	
shuttleworthii	4
simpsonii	8
smalliana	5
solonis (longii)	1
tiliaefolia	2
treleasei	2
B. *Muscadinia*	
munsoniana	3
rotundifolia	
wild	6
cultivars	5
Scuppernong	
Lucida	
Higgins	
Bountiful	
Creek	
other	2
'male'	
'trayshed'	
C. Asian *Euvitis*	
amurensis	3
coignetiae	1
flexuosa	1
piasezkii (pagnucci)	1
thunbergii	3
D. *Vitis vinifera*	
wild	27
cultivars	9
Anab-e-Shahi	
Ohanez	
Aramon	
Pagadebito	
Choultu Red	
Chardonnay #8	
Fetyaska	
French Colombard	
Malvasia bianca	
E. Interspecific hybrids	
039-16 *vinifera* × *rotundifolia*	1
043-43 *vinifera* × *rotundifolia*	1
044-4 *vinifera* × *rotundifolia*	1
171-6 *rufotomentosa* × *vinifera*	1
122-4 1613 × *rupestris* 'Metallique'	1
Y14-56 *rotundifolia* × *vinifera*	1
Tachikawa (parentage unknown)	1

lighting was used in winter and spring to maintain long days and high light intensity. The plants were fertilized regularily and insect outbreaks were controlled without systemic insecticides.

Sampling technique

The vines were first sampled for virus presence 5 months after graft inoculation by ELISA. All shoot tips from above and below the graft union were pooled and a 1.0 g sample was selected. The samples were placed in chilled mortars on ice. The plant material was triturated with a pestle in 2.5 ml of phosphate grinding buffer plus 2.5 ml 2.5 % nicotine (v/v) (JIMENEZ 1980). The homogenate was stored at −20 °C until used, but no samples were frozen longer than 72 h.

ELISA materials and procedures

The antiserum, prepared by JIMENEZ (1984), had a dilution end point of 1 : 8192. The immunoglobin fraction of the antiserum was purified as outlined by CLARK and ADAMS (1977) and conjugated to alkaline phosphatase (Sigma Type VII # P-5521) with 386 active units/ml of immunoglobin.

The polystyrene microtiter plates (Dynatech # 1223-19 lot # 112079) and the enzyme substrate (Sigma 104 Phosphatase Substrate Pellets # 104-105) were each from a single lot. The buffers used were prepared according to CLARK and ADAMS (1977), with modifications according to JIMENEZ (1980).

A double antibody sandwich procedure (CLARK and ADAMS 1977) was used. Each step involved the addition of 200 μl of reagent/well, and incubation was followed by washing 3 times for 3 min each in phosphate buffered saline plus 0.05 % Tween-20 (v/v). Plates were first incubated with coating immunoglobin in coating buffer at a concentration of 1.0 μg/ml for 4 h at 37 °C. Samples were then added and incubated for 20 h at 4 °C, after which alkaline phosphatase-labelled immunoglobin was added in conjugate buffer at a dilution of 1 : 1000 and incubated for 4 h at 33 °C. Finally, the enzyme substrate, p-nitrophenyl phosphate, in substrate buffer at a concentration of 0.8 mg/ml, was added and incubated at room temperature. After 1 h the resulting reaction was analyzed with a Titertek Multiskan Type 3100 colorimeter at 405 nm. Plates were then incubated for 24 h, after which they were analyzed again to eliminate any false negative values from the 1 h substrate reaction.

Each sample was placed in duplicate wells. Each plate included a known healthy control, *rupestris* cv. St. George, a known infected control, *vinifera* cv. Cabernet Sauvignon, and a phosphate buffered saline control. The outside wells were not used due to their well-known inconsistencies (CLARK 1981; CARDIN *et al.* 1984).

We employed a four step screening procedure consisting of two ELISA tests, with two sets of results obtained from each test. The first ELISA test was performed 5 months after graft inoculation and results were recorded after both a 1 h and a 24 h substrate reaction. The second ELISA test was performed 2 months later, and only on accessions in which no more than one vine had previously shown a positive ELISA absorbance value. In addition to absorbance values, the success of the graft unions and the vigor of both candidate and inoculum plants was rated.

Results

The established basis for judging infection in a candidate plant with ELISA has been to consider a sample infected if its absorbance value is greater than 2 times the

healthy control (GONSALVES 1979; RAMSDELL *et al.* 1979; ENGLEBRECHT 1980; SHANMUGANATHAN and FLETCHER 1982). However, in this study the absorbance values of the various control vines covered a very wide range, presumably due to their genetic diversity. Because the controls differed so markedly, the use of the established procedure would have resulted in a vine from one accession being judged infected while another with the same absorbance value was judged uninfected, solely because their respective controls had such differing absorbance values. We sought to avoid this inconsistency by developing a criterion that could be applied more uniformly. The method we arrived at relies on the pooling of related accessions into groups such that all ELISA absorbance values obtained within a group are considered as a population for statistical purposes.

The accessions were grouped according to their geographic and genetic affiliations, as shown in Table 1. The absorbance values of the inoculated plants in each group were divided into two sets — 1 h values and 24 h values. These sets were further divided into three subsets: first test values (5 months), second test values (7 months), and combined first and second test values. Histograms were made for each of these six subsets. All of the histograms described bimodal distributions with peaks near 0.100 and 1.999 OD for 1 h substrate reactions, and 0.200 and 1.999 OD for 24 h substrate reactions, with many scattered points between the extremes. The low ends of the histograms were selected as defining populations of uninfected values. The cut-off points chosen were 0.150 for 1 h values and 0.300 for 24 h values. Absorbance values of the uninoculated control plants were not included to avoid skewing the populations towards the low end of their range.

Table 2

Delineation points for judging virus resistance within accession groupings · Values in OD 405 nm

Grenzwerte zur Beurteilung der Virusresistenz in den einzelnen Testgruppen · Werte als OD 405 nm

Accession	First test		Second test		Combined	
	1 h	24 h	1 h	24 h	1 h	24 h
North American *Euvitis*	0.105	0.266	0.099	0.151	0.104	0.258[1])
Muscadinia	0.081	0.190	0.065	0.145	0.076	0.181
Asian *Euvitis*	0.069	0.306	0.064	0.141	0.067	0.280
Vitis vinifera	0.079	0.221	0.086	0.245	0.081	0.225
Interspecific hybrids	0.091	0.226	0.060	0.213	0.081[1])	0.223

[1]) Combined values were used for the delineation points except in these two cases in which the F values were significant and so the appropriate first test or second test delineation point was used.

The selected populations for each subset were then treated as normal distributions and an upper confidence limit was calculated for each. This confidence limit provided a delineation point which could be used to judge all accessions within a subset. If the absorbance value of an accession candidate was below the delineation point, then it could be considered uninfected with 95 % confidence.

We were concerned that the delineation points derived from the smaller second test populations would not be as accurate as the first test delineation points. This concern led to the creation of the combined first and second test populations. Analysis of variance was performed to determine if there was a significant difference among the first

Table 3

Accessions within which one plant produced a positive ELISA absorbance value

Testgruppen, in denen einzelne Pflanzen ELISA-positiv reagierten

Accession	Number of plants tested	Intensity of positive absorbance value[1]) First test		Second test		Comments
		1 h	24 h	1 h	24 h	
A. *Euvitis*						
lincecumii # 1	4	++++	++++	+++ +	++++	No problems
monticola # 7	4	----	+	+	++	Positive plant dead above graft, other 3 weak
shuttle-worthii # 1	4	++	++++	++++	++++	Graft separated on 1 negative plant
vinifera # 2	4	----	----	++	++++	Second plant borderline positive
vinifera # 9	3	+	++++	+	++++	Second plant borderline positive
vinifera # 10	3	----	----	+ +	++ + +	No problems
B. Interspecific hybrids						
043-43 (VR)	2	----	----	----	+	No problems

[1]) below delineation point.
+ between delineation point and 0.499 OD.
++ 0.500—0.999 OD.
+++ 1.000—1.499 OD.
++++ > 1.500 OD.

test, the second test, and the combined first and second test populations. If the F value obtained was not significant, then the combined population delineation point was applied to both tests (see Table 2). The delineation points were then used to judge the accessions as infected or uninfected through the four step screening process. The results are shown in Tables 3 and 4.

Discussion

Efforts to identify resistance to GFV began with PETRIE (1937), who noted that not all *vinifera* cultivars were equally affected by 'l'arricciamento'. VUITTENEZ (1957) tested *Vitis* species from both North America and Asia, as well as the *vinifera* cultivars Chardonnay and Traminer, but did not identify any sources of resistance. JIMENEZ (1980)

Table 4

Accessions within which no positive absorbance values were detected by ELISA

Testgruppen, in denen keine positiven ELISA-Werte gefunden werden konnten

Accession	Number of plants tested	Vineyard location	UC Davis number	Comments
A. *Muscadinia*				
munsoniana # 3	2	Z5 (1)	54112	2 weak plants
rotundifolia # 2	3	KL52 (3, 4)	b55-24	2 weak plants
rotundifolia # 5	3	KL52 (9, 10)	b55-29	2 weak plants, 1 plant dead above graft
rotundifolia cv. Bountiful	4	KL59 (1, 2)	7701	No problems
B. Interspecific hybrids				
Y14-56	3	M12 (53)	V57	1 weak plant, 2 live plants with separated grafts
039-16	3	M32 (15)	N71	No problems
C. *Euvitis*				
shuttleworthii #3	3	Z18 (1)	54103	2 plants dead above graft
vinifera #4	3	M3 (18)	1140	No problems

graft inoculated a range of *Vitis* germplasm, emphasizing *vinifera* cultivars, and identified several sources of resistance. We included sources of previously reported resistance in our study and found none of them to be actually resistant. Our survey did reveal three clear sources of resistance to GFV: a *rotundifolia* cultivar, a *vinifera* x *rotundifolia* (VR) hybrid, and a wild Middle Eastern *vinifera* accession.

The species used in this study included representatives from the three centers of origin of *Vitis:* America, the Middle East, and Asia (OLMO 1976). We emphasized Middle Eastern *vinifera* accessions because of the possibility that GFV and *vinifera* evolved together in the Middle East (HEWITT 1976; OLMO 1976). If this were true, then resistance to GFV might be expected in wild *vinifera* accessions from this area. Ideally all Middle Eastern *vinifera* populations should be screened. However, this was not possible, but we examined 25 *vinifera* accessions collected by H.P. OLMO in Afghanistan and Iran in 1954 (H.P. OLMO, personal communication). In addition to North American and Asian *Vitis* species, we also included interspecific hybrids which have exhibited field resistance to infectious degeneration thought to be the result of resistance to *X. index* feeding.

Only accessions within which no virus can be detected may be considered resistant to GFV. However, because labelling or propagating errors are possible, we have identified accessions within which only one positive absorbance value was obtained as being possibly resistant (Table 3). These accessions will be retested in the future to clarify their status. The accessions in which resistance to GFV is more likely are presented in Table 4, and they will be discussed individually. Both plant vigor and graft success

were noted, as both of these factors are important for successful transfer, replication and detection of virus in the host plant (MATTHEWS 1981).

There were 4 *Muscadinia* accessions within which no positive absorbance values were detected. The absence of positive values could have been the result of graft incompatibility, poor growing conditions for *Muscadinia* species, or nonhost resistance, but it is not likely to represent host plant resistance.

The subgenera *Muscadinia* and *Euvitis* are distinct both genetically and morphologically. Furthermore, it is thought that GFV evolved with *vinifera* in the Middle East (HEWITT 1976; OLMO 1976), rather than in North America, the home of *Muscadinia.* Thus it is likely that resistance found in the *Muscadinia* species is distinct from that found in *vinifera.* It is reasonable to suppose that the resistance to GFV present in the *Muscadinia* species is the result of gross incompatibility between the virus and the *Muscadinia* cells and not the result of an evolved cellular defense against the virus. This type of passive resistance has been called 'nonhost resistance' (HEATH 1981).

For three of the *Muscadinia* accessions in Table 4 (*munsoniana* # 3, *rotundifolia* # 2 and *rotundifolia* # 5) there are reasons to doubt whether they are truly resistant genotypes. Either the vines were weak or the graft unions were in question. Both of these problems can affect virus infection. If a plant is weak, virus replication and spread will be impaired (MATTHEWS 1981), leading to false negative values in the ELISA test. Furthermore, if a plant is dead above the graft union there is a chance that the virus, although supposedly systemic, might not be detected in the lower leaves. Such an occurrence would not be due to resistance, but rather to the absence of virus movement. However, we did observe many cases in which a plant that was dead above the graft union still had high absorbance values in leaves below the graft.

All 4 vines of Bountiful, a *rotundifolia* cultivar grown in the southeastern United States, were vigorous and the graft unions were sound. Bountiful was the most vigorous *Muscadinia* accession tested, and propagation and cultivation were less difficult than with other *Muscadinia.* This is an excellent example of nonhost resistance to GFV.

Y14-56 is a *rotundifolia* × *vinifera* (RV) hybrid. This is one of the few such crosses with *rotundifolia* as the female parent. It was found at the University of California, Davis by JELENKOVIC and OLMO (1968) in a *rotundifolia* seedling block that was surrounded by *vinifera* cultivars. Its parentage is (*rotundifolia* cv. Thomas × *rotundifolia* 'trayshed') × O.P. *vinifera.* Of the 3 vines screened, 1 was weak and 2 had grafts that had separated by the time of second testing. Graft success is not necessary for virus transfer from infected plant to uninfected plant (KUNKEL 1938; GIBBS and HARRISON 1976; GOHEEN, unpublished). If a graft fails, however, inoculation may not occur, and vines with failed grafts must remain questionable. As with the *Muscadinia* accessions, this RV hybrid could possibly have nonhost resistance to GFV.

039-16 is a *vinifera* X *rotundifolia* (VR) hybrid. Its parentage is *vinifera* cv. Hunisa × *rotundifolia* 'male #1', and it was made between 1948 and 1950 by PATEL and OLMO (1955) as part of a series of VR hybrids. Hunisa was not tested in this survey, but given the susceptibility to GFV of all *vinifera* cultivars indexed in the grape germplasm importation program at UC Davis (GOHEEN, unpublished), the *rotundifolia* parent must be considered responsible for the resistance in 039-16. This VR hybrid is part of a rootstock breeding program at Davis, and unpublished results show that 039-16 has field resistance to infectious degeneration. This field resistance has heretofore been thought to be due to feeding resistance because feeding studies with *X. index* show 039-16 to have high resistance (LIDER, unpublished). The possibility of combined resistance to GFV and *X. index* makes this accession very interesting and heightens its potential as a GFV-resistant rootstock.

Shuttleworthii #3 is a Floridian *Euvitis* species whose range overlaps that of *munsoniana* and *rotundifolia*. 2 of the *shuttleworthii* #3 plants were weak and in 2 cases the vines were alive only below the graft union. While these conditions could have accounted for the absence of GFV, resistance is also a possibility. As an American *Euvitis* species *shuttleworthii* would not be expected to have evolved resistance to GFV. However, because of its overlapping with *Muscadinia* species, it is possible that this particular *shuttleworthii* has some *Muscadinia* parentage and may indeed have nonhost resistance to GFV.

Vinifera #4 is from a seedling population collected in 1954 in Adhai, Afghanistan (H. P. OLMO, personal communication). Each of the 3 plants of this accession had good vigor and successful grafts. *Vinifera* #4 represents an excellent example of host plant resistance to GFV. The discovery of resistance in *vinifera* #4 suggests that other sources of resistance to GFV may also be found within populations of Middle Eastern *vinifera* and its cultivars.

Of the 8 accessions listed in Table 4, 3 in particular warrant further consideration: the VR hybrid 039-16, *rotundifolia* cv. Bountiful, and the Middle Eastern *vinifera* #4. For these accessions there is no reason to question their resistance to GFV. We are now investigating the nature and the inheritance of resistance in the resistant genotypes we have identified. These investigations will help us to better understand the nature of the disease caused by GFV. We expect that the incorporation of these resistant genotypes into breeding programs, particularly in combination with *X. index* resistant genotypes, will lead to a new generation of rootstocks for GFV-infested vineyards.

Summary

A diverse array of *Vitis* germplasm was screened to identify sources of resistance to grapevine fanleaf virus (GFV). The 173 accessions screened included *Vitis* species, cultivars, and interspecific hybrids. Since *Vitis vinifera* and GFV are thought to have a common origin in the Middle East, particular attention was paid to this species — 27 Middle Eastern *vinifera* accessions and 9 *vinifera* cultivars were surveyed. In addition, North American accessions of 24 *Euvitis* species and 2 *Muscadinia* species were tested, including cultivars of *rotundifolia*, as were accessions of 5 Asian species. The interspecific hybrids included 3 *vinifera* × *rotundifolia* (VR) hybrids known to be resistant to the feeding of *Xiphinema index*, the nematode vector of GFV. The vines to be tested were approach grafted to infected Cabernet Sauvignon vines and subsequently screened for the presence of the virus by ELISA. 3 GFV-resistant accessions were identified — a Middle Eastern *vinifera*, *rotundifolia* cv. Bountiful, and one of the VR hybrids. Several *vinifera* accessions (including some cultivars) previously reported to be GFV-resistant were susceptible in this study. These results suggest that two forms of GFV resistance, host plant resistance and nonhost resistance, exist in *Vitis* germplasm.

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Literature cited

ALFARO, A.; GOHEEN, A. C.; 1974: Transmission of strains of grapevine fanleaf virus by *Xiphinema index*. Plant Disease Rep. **58**, 549—552.

BOUBALS, D.; PISTRE, R.; 1977: Résistance de certaines Vitacées et des porte-greffes usuels en viticulture au nématode *Xiphinema index* et à l'inoculation par le virus du court-noué (GFLV). Génétique et Amélioration de la Vigne. IIe Symp. Intern. Amélior. Vigne, Bordeaux, 199—207. INRA, Paris.

BOUQUET, A.; 1980: Resistance to grapevine fanleaf virus in Muscadine grape inoculated with *Xiphinema index*. Plant Disease **65**, 791—793.

— —; DANGLOT, Y.; 1983: Recherche de porte-greffes de vigne résistant à la transmission du virus du court-noué (GFV) par le nématode *Xiphinema index* THORNE and ALLEN. I: Application de la méthode ELISA à la réalization d'un test rapide de sélection. Agronomie **3**, 957—963.

— —; HEVIN, M.; 1978: Green-grafting between Muscadine grape (*Vitis rotundifolia* MICHX.) and bunch grapes (*Euvitis* spp.) as a tool for physiological and pathological investigations. Vitis **17**, 134—138.

BOVEY, R.; 1980: Control of virus and virus-like diseases of grapevine: Sanitary selection and certification, heat therapy, soil fumigation and performance of virus-tested material. Proc. 7th Intern. Conf. Viruses and Vectors of Grapevines, Niagara Falls, Canada, 299—309.

CARDIN, L.; DEVERGNE, J. C.; PITRAT, M.; 1984: Dosage immunoenzymatique (ELISA) du virus de la mosaïque du concombre. I. Aspect méthodologique. Agronomie **4**, 125—135.

CLARK, M. F.; 1981: Immunosorbent assays in plant pathology. Ann. Rev. Phytopathol. **19**, 83—106.

— —; ADAMS, A. N.; 1977: Characteristics of the microplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. J. Gen. Virol. **34**, 475—483.

ENGLEBRECHT, D. J.; 1980: Application of the enzyme-linked immunosorbent assay for the detection of grapevine fanleaf virus. S. Afr. J. Enol. Viticult. **1**, 103—106.

GIBBS, A.; HARRISON, B.; 1976: Plant Virology: The Principles. pp. 137—158, Behavior of viruses in plants. Edward Arnold Press, London.

GOHEEN, A. C.; LUHN, C. F.; 1973: Heat inactivation of viruses in grapevines. Riv. Pathol. Veg. **9**, 287—289.

GONSALVES, D.; 1979: Detection of tomato ringspot virus in grapevines: A comparison of *Chenopodium quinoa* and enzyme-linked immunosorbent assay (ELISA). Plant Disease Rep. **63**, 962—965.

HARTMAN, H. T.; KESTER, D. E.; 1975: Plant Propagation: Principles and Practices, 3rd ed. Prentice-Hall Inc., Englewood Cliffs, New Jersey.

HEATH, M. C.; 1981: Nonhost resistance. In: STAPLES, R. C.; TOENNIESSEN, G. H. (Eds.): Plant Disease Control, 201—217. John Wiley and Sons, New York.

HEWITT, W. B.; 1976: On the origin and distribution of *Vitis* and the virus diseases of the grapevine. Proc. 6th Intern. Conf. Viruses and Vectors of Grapevines, Cordoba, Spain, 3—4.

— —; RASKI, D. J.; GOHEEN, A. C.; 1958: Nematode vector of soil-borne fanleaf virus of grapevines. Phytopathol. **48**, 586—593.

JELENKOVIC, G.; OLMO, H. P.; 1968: Cytogenetics of *Vitis*. III. Partially fertile F_1 diploid hybrids between *V. vinifera* L. × *V. rotundifolia* MICHX. Vitis **7**, 281—293.

JIMENEZ, F.; 1980: Resistance to Fanleaf Virus among Cultivars and Grape Species. M. S. Thesis. Univ. Calif., Davis.

— —; 1984: Isolation, Purification and Quantitative Serology of Grapevine Fanleaf Virus. Ph. D. Thesis. Univ. Calif., Davis.

KUNDE, R. M.; LIDER, L. A.; SCHMITT, R. V.; 1968: A test of *Vitis* resistance to *Xiphinema index*. Amer. J. Enol. Viticult. **19**, 30—36.

KUNKEL, L. O.; 1938: Contact periods in graft transmission of peach viruses. Phytopathol. **28**, 491—497.

MATTHEWS, R. E. F.; 1981: Plant Virology, 2nd ed. Academic Press, New York.

OLMO, H. P.; 1976: Grapes: *Vitis, Muscadinia* (Vitaceae). in: SIMMONDS, N. W. (Ed.): Evolution of Crop Plants, 294—298. Longman, London.

PATEL, G. I.; OLMO, H. P.; 1955: Cytogenetics of *Vitis:* I. The hybrid *V. vinifera* × *V. rotundifolia*. Amer. J. Bot. **42**, 141—159.

PETRIE, L.; 1937: Transmissione del virus dell'arricciamento della vite attraverso i tessuti di una varietà resistente. Reconditi delle sedute della reale Academia Nazionale dei Lincei. Classe di Science Fisiche, Matematiche e Naturali **25**, 413—416.

Ramsdell, D. C.; Andrews, R. W.; Gillet, J. W.; Morris, C. E.; 1979: A comparison between enzyme-linked immunosorbent assay (ELISA) and *Chenopodium quinoa* for detection of peach rosette mosaic virus in 'Concord' grapevines. Plant Disease Rep. **63**, 74—78.

Raski, D. J.; Goheen, A. C.; Lider, L. A.; Meredith, C. P.; 1983: Strategies against grapevine fanleaf virus and its nematode vector. Plant Disease **67**, 335—339.

Shanmuganathan, N.; Fletcher, G.; 1982: Enzyme-linked immunosorbent assay to detect fanleaf virus in grapevines grown in containers. Plant Disease **66**, 704—707.

Taylor, R. H.; Woodham, R. C.; Allan, A. W.; 1967: Green grafting: a useful technique for detecting grapevine viruses. Austral. J. Exp. Agricult. Anim. Husb. **7**, 91—95.

Vuittenez, A.; 1957: Inoculation de différentes espèces de *Vitis* par les virus du groupe de la dégénérescence infectieuse. Application au diagnostic de la maladie. IVe Congr. Intern. du Lutte contre les Ennemis des Plantes. Hambourg, 1957. Comptes Rendus (Braunschweig) **1**, 361—366.

Weischer, B.; 1980: The host-parasite relationships between the vector nematode *Xiphinema index*, and some *Vitis* spp. Proc. 7th Intern. Conf. Viruses and Vectors of Grapevines, Niagara Falls, Canada, 139—146.

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