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The Vitis vinifera × V. rotundifolia Hybrids as Phylloxera Resistant Rootstocks

by

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Introduction

The native American grape species *rotundifolia* of the southeastern United States can serve as important parent material in breeding new cultivated varieties. The remarkable resistance or even immunity of this species to a wide range of devastating diseases and insects of the *vinifera* grape have been mentioned (10). A long term project is under way to attempt to transfer these resistant qualities to the *vinifera* grape.

In the past, *rotundifolia* has been neglected in grape improvement because of certain barriers intrisic in the species. First, varieties of the species were not widely disseminated because it could not be rooted from dormant cuttings. Interplanting with male vines to provide for cross pollination was necessary. *Rotundifolia* starts growth much later and blossoms several weeks after *vinifera*. Most of the earlier varieties disseminated were very late in maturity, and were not winter hardy. Difficulty was encountered in crossing with other grape species, since hybridization is only rarely accomplished unless the *rotundifolia* is used as the male parent. Although the F_1 hybrids between *vinifera* × *rotundifolia* (VR hybrids) are usually vigorous, they are often highly sterile and considerable effort must be expended to obtain more advanced generations or backcrosses. With the use of newer techniques and a better understanding of the cytogenetic background, once serious impediments are now being resolved.

RAVAZ (14) has mentioned that the *rotundifolia* is the species of vine least attacked by phylloxera, and that its roots are always or nearly always immune, it is a rarity to even find a lesion.

The absence of the leaf gall form of the phylloxera in California necessitates that all tests of resistance must be made with the root form only. This presents no serious obstacle, especially since these two phases of the insect have been shown to be mutually related, and depending on environmental conditions one can easily revert to the other. Even if it were possible to use the leaf form in resistance studies, no great advantage would ensue. From the practical viewpoint the longevity of the plant *vis a vis* phylloxera is determined by the accumulating damage to the root system and not to the more ephemeral and seasonal galling of the leaves. It is also well known that tolerance of the root system is often inversely related to the formation of leaf galls. *V. rupestris* du Lot, a stock with a long history of satisfactory tolerance as a root, may become so badly galled in nursery mother plantations that it seriously affects the growth of the shoots and reduces the yield of marketable cuttings in some areas of southern Europe.

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The present report deals with the reaction of some first generation VR hybrids and their derivatives to the root form of phylloxera, in greenhouse and field tests. Preliminary experiments with these new hybrids as rootstock vines are also reviewed.

Materials and Methods

Since the VR hybrids had been observed to show a wide range of root lesion injury from phylloxera attack, they appeared ideal to test for any possible racial differences in the phylloxera.

Hence, phylloxera from five different vineyard locations were collected. Infected rotos from declining *vinifera* vineyards were sampled for laboratory study during the period Sept. 27, 1956 to March, 15, 1957. The locations were as follows:

1. Yountville, Napa County.
2. Alexander Valley, Sonoma County
3. Asti, Sonoma County
4. Exeter, Tulare County
5. Davis, Yolo County

The first three localities are in the coastal region north of San Francisco, in an area longest infected with phylloxera and in which the use of phylloxera resistant rootstocks is now universal. Phylloxera was first identified near Sonoma in 1873 (2). Infection in the Exeter vineyard goes back about 50 years, and in the Davis site about as long.

In contrast to most European localities, the destruction of *vinifera* vineyards in California has been extremely slow. Some plantings known to be infected for 20 or even 30 years are still profitable. The deep and fertile soils allow extensive development of the root system. However as declining vineyards are replanted, the degree of resistance of the rootstock becomes increasingly important.

In order to maintain active laboratory cultures of phylloxera for examination and to be used later for inoculation of test plants several methods were used. Phylloxerated roots freshly dug from vineyards were inserted by their bases into 3—4 inches of wet peat moss in wide-mouthed gallon jars. The tops were covered with cheesecloth and the containers placed in an incubator in the dark with a temperature range of 70—75^0 F. Active proliferation of the insects occurred within a month's time, and the roots callused and sometimes new rootlets emerged. With this simple method phylloxera was kept thriving for from 2 to 3 months. Beyond this interval, the colonies began to decline, and there was a concurrent increase of fungal and mite populations on the roots.

A second method was to cleanly wash the root systems of one-year old seedlings vines grown in pots of sterilized soil. The vines were then placed with the lower half of the root system immersed in jars containing 2 liters of Hoagland's nutrient solution. The jars were wrapped with aluminium foil to exclude light, and the vine was supported at the stem by a loosely fitting linoleum cover. Phylloxera colonies were established within two weeks, and developed in localized areas some distance from the liquid surface, but not in the upper drier air of the jar. Once again, after two or three months the phylloxera colonies died off.

Daily observations of the phylloxera cultures from the five different sources failed to uncover any differences in gross morphology. As to behavior of the insects, nothing unusual was noted except the appearance of alates in one collection.

One winged form was first observed on March 24, 1957, from a root of the Alexander Valley sample taken on January 18. A dozen nymphs and prenymphs were counted on the same root, and by March 30 four more winged insects had emerged. All of the winged migrants were isolated individually as they appeared and were placed in Petri dishes. No oviposition was observed. DAVIDSON and NOUGARET (6) first noted nymphs appearing on June 14, but their studies were under cooler cellar temperatures. In the greenhouse, no instances of leaf gall formation were ever observed on the vines, either *vinifera* or hybrid. The complete absence of this stage of the phylloxera in all experimental cultures remains an enigma. Only two separate instances of phylloxera leaf galling have been reported in the whole history of grape growing in California.

For the greenhouse tests, galvanized sheet metal tanks 44 × 96 inches were set on benches 30" high and used as plant containers, with a surrounding reflexed rim of about 1" in which a film of oil was kept to keep the phylloxera from migrating. The tank to accomodate rooted vines was about 15" in depth, whereas for testing of seedlings plants, a shallow tank of only 6" depth gave much quicker buildup and infestation. The tanks were equipped with a sloping bottom and the drainage water was collected from a 3/4" spout and emptied into a bottle. Several inches of coarse gravel was first placed on the bottom of the tank to insure good drainage, then steam sterilized Yolo heavy loam soil was used in which to plant the vines. This soil cracked considerably after watering and provided a good medium for the movement of the radicicola.

Plants of the VR hybrids and the *vinifera* controls were grown from cuttings in a field nursery, in previously fumigated soil. They were dug and washed clean in fresh water, and stored in a cold room until ready for planting in the greenhouse tanks.

In the greeenhouse tank cultures, the rooting of the VR hybrids were planted in 2 randomized blocks along with the *vinifera* varieties used as controls. The VR hybrids were delayed in the start of active growth as they resembled the *rotundifolia* in requiring a higher mean temperature for active shoot and root growth, as well as recovering less well after replanting. Only a few hybrid rootings failed to grow, and this was apparently due to infection with *Dematophora*.

The first greenhouse test planting was made on January 23, 1957 in the tank "A" and consisted of 1-yr. old rooted vines, of the following VR hybrids.

Almeria × *rotundifolia* 3; 5 clones
Hunisa × *rotundifolia* 3; 8 clones

The clones were selected at random from a larger population of vines. For the origin and description of these vines, see PATEL and OLMO (1955).

As controls, rootings of the *vinifera* 'Sultanina' taken from the same nursery were used. Two rootings of each hybrid were selected for uniformity, permitting two randmized blocks to be used. Hybrid vines alternated with the susceptible *vinifera* controls, which permitted a rather uniform distribution of phylloxera throughout the soil mass. The plants were placed about 9 × 20 cm, so as to allow close contact of the roots. Phylloxera inoculation was done at planting time, by placing an infested grape root about 10 cm long in contact with the root system of each plant. The Exeter phylloxera collection was used.

A second tank "B" was prepared and planted on February 9, 1957. The same hybrid combinations were used, but different individual VR vines. The susceptible control variety *vinifera* was 'Flame Tokay'. In this tank the phylloxera collection was from the Alexander Valley.

Greenhouse temperatures reached a maximum of 85° F and a minimum of 65° F during the period. The tests were terminated after seven months, by which time there was heavy damage to the *vinifera* control. The tanks were filled with water and let stand overnight. The vines with intact root systems were then easily pulled one by one from the slurry, and washed clean with fresh water to make them ready for examination. Preliminary experiments indicated a good measure of root injury could be obtained by counting the nodosities and tuberosities on all new roots that had developed, using only those that were greater than 1 mm in diameter. The total root length examined could also be estimated. At the time of planting, the roots had been shortened back to about 1" stubs, and the new roots arising from the terminal portion of these were used for the measurements (Fig. 1). The results are summarized in Table 1. A few rootings failed to grow and those that produced less than 25 cm of new roots for scoring were eliminated.

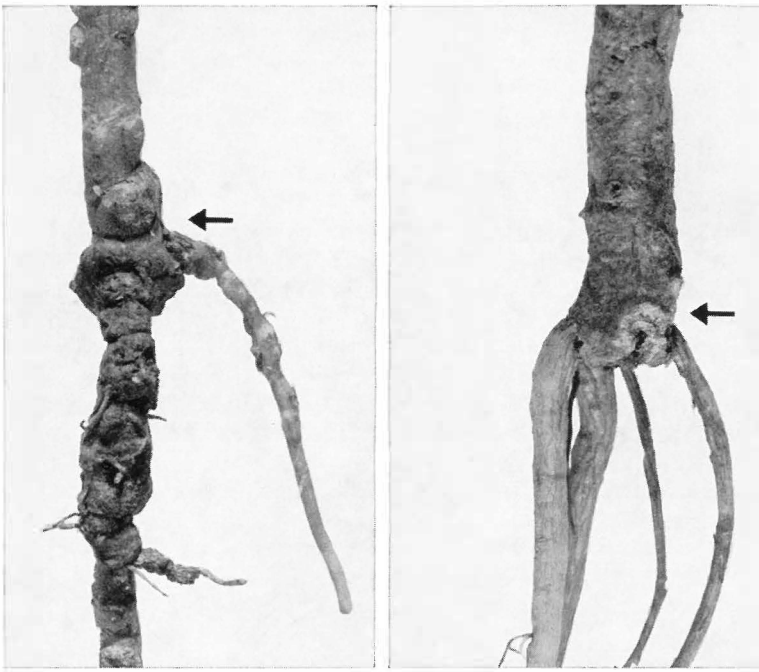

Fig. 1. A. Portion of root system of *vinifera* 'Hunisa' showing abundant necrotic lesions (x 2).

B. The VR clone 043-15, with no insects or lesions.

Arrow indicates where 1 year old root was shortened before planting for test in tank.

Results

The large variation in the number of lesions between vines (clones) of the same parentage was not anticipated in the VR hybrids. Because of the limited number of rootings available from each plant at this stage of the study, it was impossible to provide more than a single replication of each clone within the tank. Thus clone 041-14 from the standpoint of lesion number alone, was as susceptible as the *vini-*

Table 1

Root lesions on VR hybrids and *vinifera*

	Tank A					Tank B			
Parentage	Vine	N	T	Roots cm		Vine	N	T	Roots cm
Almeria	041-7	4	0	75		041-5	0	0	235
×	-13	0	0	40		-10	20	8	157
rot. 3	-29	2	1	200		-14	76	68	25
	-39	9	2	235		-37	0	0	60
	-48	8	0	60		-46	0	0	175
						-50	5	10	40
	Mean	4.8	0.6	122.0			16.8	14.3	115.3
Hunisa	042-13	17	2	205		042-17	0	0	145
×	-20	5	0	270		-35	1	0	755
rot. 3	-32	10	16	157		-39	2	0	256
	-37	4	0	256		-50	29	0	55
						-58	3	0	630
	043-15	5	0	200		043-1	3	0	315
	-16	7	0	130		-13	44	43	70
	-28	25	0	80		-20	6	7	522
	-43	18	12	132		-49	0	6	85
						-53	3	9	485
						-58	0	0	100
	Mean	11.4	3.8	178.7			8.3	5.9	310.7
V. vinifera	1	30	73	357	*V. vinifera*	1	20	57	270
Sultanina	2	44	183	187	Flame Tokay	2	48	73	315
	3	16	154	325		3	18	82	225
	4	34	164	245		4	25	127	207
	5	36	121	206		5	29	100	220
	Mean	32.0	139.0	264.0			28.0	87.8	247.4

Each entry is mean of duplicate sample planted in randomized block
N = mean number of nodosities per 100 cm of root
T = mean number of tuberosities per 100 cm of root

fera control. However, the means of the parentage groups are significantly different, both sets of VR hybrids. Almeria × *rotundifolia* 3 and Hunsia × *rotundifolia* 3, are much less affected than the *vinifera* controls. As to type of lesion, tuberosities are absent in most of the VR hybrids, but the *vinifera* controls are uniformly high.

Four out of 11 clones in the Almeria hybrids and 2 of 19 in the Hunsia hybrids were free of lesions. These may be in the "immune" class, and possibly do not support phylloxera at all. These tests are being extended to see if (1) phylloxera can survive at all on such roots, (2) if any reproduction of the insect on these roots is possible.

Analyses of variance of lesion number, using the original data, shows no significant differences that can be attributed to the *vinifera* parent of the VR hybrid. There appear to be no major genetic differences for relative susceptibility betweeen the two *vinifera* parents, Almeria and Hunisa. Root growth of some of the VR hybrids, as measured by total length, is superior to the *vinifera* controls, but there is extreme variation between VR clones.

If we consider lesion number alone, the mean values of the VR hybrid more nearly approach the 0 of *rotundifolia* than they do the *vinifera* values, indicating some dominance of the *rotundifolia*. However, it is equally evident that more than a single major gene is involved in the inheritance of resistance,

The data are nonetheless convincing that the VR hybrids are highly tolerant and some may be immune. A considerable number of plants in the F_1 progenies do not form root lesions, although it is not certain whether the phylloxera can feed on the roots occasionally, but fail to provoke hyperplasia. A factor of considerable importance appears to be the structure of the root cortex and the lack of fissuring and irregular sloughing off characteristic of *vinifera*. In a study of the anatomical stem characters of VR hybrids, WILLIAMS (15) noted that "the cortex in the hybrids shows less fixation of a definite character than any other part of the stem, varying from a close resemblance to the staminate parent to a similarity to the pistillate parent. In most cases the cortex is very much like that of the *V. rotundifolia* species."

The same situation applies to the root structure, where the position and activity of the phellogen appears to play the decisive role. Invariably the VR hybrids consistently supporting large populations of phylloxera have anatomical characteristics more aproaching the *vinifera* parent. The presence and abundance of root lenticels are correlated with this pattern, as they are present when the phelloderm is well developed immediately under the epidermis, as in *rotundifolia* and the most lesion-free hybrids. These observations emphasize the importance of the anatomical basis of phylloxera resistance. The VR hybrids thus offer excellent material for a detailed and critical study of these factors, since there is a wide range of anatomical patterns.

Although the recording of nodosities and tuberosities gives a rough quantitative measure of the ability of the phylloxera to cause root lesions, it is the degree of injury of each lesion that is even more important and of which we have no relative measure. Thus it is reasonable to suppose a single deep and highly necrotic tuberosity may be more detrimental than several more superficial lesions that have become limited in extension by corky cell growth. It has been noted that the VR hybrids with the highest recorded frequency of lesions, for example 031-14 or 043-13, did not show the same degree of weakening in top growth as the *vinifera* controls, even though the number of lesions per unit of root growth is as high or higher than *vinifera*. We are now of the opinion that a better measure of phylloxera resistance would be to measure the total growth of the plant, comparing infected with non-infected plants, but this would necessarily be a procedure requiring a longer period of time and needing many replications. With the tank method, a period of two years might provide satisfactory results.

Since the tank method was used to determine the lesions formed on the roots, rather than noting the phylloxera themselves, supplementary experiments were conducted so that the relative numbers of insects could be observed on the root system, to be more certain of the relationship between the injury from lesions and feeding of the phylloxera. A VR rooting was paired and planted together with a *vinifera* rooting in 3 gallon cans or clay pots. *Vinifera* was also paired with *rotundifolia* seeedlings of the cultivar 'Hunt'. The Ravaz (14) method of lining the soil mass with beach sand was utilized, and inoculation was done with a root piece. After seven months in the greenhouse, the containers were inverted and carefully emptied so the root systems could be examined immediately under the 20 × binocular on November 13—15, 1957.

One of the clones, 042-35, had also been tested in the tank B, where only a single nodosity was observed, but no tuberosities. No insects were found living on the roots of this clone in the Ravaz test. All of the paired trials successfully built up large populations of phylloxera (Alexander Valley) on the *vinifera* roots, hence all were classified as "insects abundant". Where no insects were found on the VR roots, there were also no lesions of any consequence, (Fig. 1, B) representing 5 of 13 clones used in the experiment. In three parallel tests, the *rotundifolia* variety 'Hunt' was paired with infected *vinifera*, without establishment of the insects. There was evidence that occasionally some phylloxera fed on and pierced the *rotundifolia*, but did not remain to become lodgers, nor was there any reproduction of young noticed on these plants. The results are summarized in Table 2.

Tetraploid Derivatives.

Partially fertile tetraploids of the F_1 VR sterile hybrids produced by colchicine treatment (13) were used in crossing experiments, with the idea of obtaining different dosages of *rotundifolia* and *vinifera* genomes in the tetraploid for phylloxera tests. The results of these crosses were only partially successful, as the reesults of Table 3 indicate. The N series of numbers are allotetraploids of the genomic constitution VVRR, from chromosome doubling of the F_1 VR.

Table 2

Relative numbers of phylloxera colonies on the root systems. Ravaz method.

Parentage	Clone	No insects found	Few colonies	Many colonies	Insects abundant
Hunisa × *rot.* 2	044-1		+		
	044-3	+			
	044-4	+			
	044-6			+	
	044-15		+		
	044-17		+		
Hunisa × *rot.* 3	042-35	+			
	043-2				+
	043-6				+
	043-9	+*)			
	043-15	+			
	043-30			+	
	043-50		+		
rotundifolia	'Hunt'	+			
vinifera (all cans)					+

*) Root system poorly developed, questionable rating

Table 3

Crossing results of tetraploid VR hybrids.

Female parent	Male parent	Flowers*) pollinated	Berries harvested	Seeds
N 53-2	N 53-1	230	0	0
	N 53-3	135	0	0
	N 53-32	240	0	0
	N. C. 11-178	258	5	5
	Muscat 4n	210	6	6
	Sultanina 4n	40	0	0
N 53-6	N 53-3	185	0	0
	N 53-7	95	0	0
	Muscat 4n	115	0	0
	Sultanina 4n	65	0	0
N 53-8	N 53-1	280	0	0
	N 53-3	80	0	0
	N 53-32	100	0	0
	N. C. 11-178	285	0	0
	Muscat 4n	25	0	0
	Sultanina 4n	265	36	75
N 53-13	N 53-1	140	31	26
	N 53-3	380	0	0
	N 53-32	45	0	0
	Muscat 4n	250	23	19
	Sultanina 4n	45	22	28
N 53-28	N 53-1	140	0	0
	N 53-3	500	0	0
	N 53-32	540	0	0
	N. C. 11-178	140	0	0
	Muscat 4n	140	0	0
	Sultanina 4n	620	7	10
N 53-56	N 53-1	40	0	0
	N 53-3	40	0	0
	N 53-32	80	0	0
	Muscat 4n	40	0	0
	Sultanina 4n	135	1	1

*) The largest clusters used had from 20 to 50 flowers each.
N. C. 11—178 = a tetraploid *rotundifolia* from North Carolina.
Muscat = Muscat of Alexandria

The tetraploid VR hybrids are highly self and cross sterile. However, the great range of variability in this respect between plants of the same F_1 parentage is remarkable, and it is impossible to make generalizations on this point until more is understood of the chromosome and genetic segregation in these plants. N 53-2, for example produced seed and viable hybrids plants with both tetraploid *vinifera* Muscat and tetraploid *rotundifolia* N. C. 11-178, but not with pollen of sib plants. The vine N 53-6 was completely sterile. The female variety N 53-13 was succesfully crossed with N 53-1, but the many other combinations were failures.

Table 4

Root lesions on tetraploid seedling vines of the constitution VVVR.

Parentage	Pot. No.	N	T	Roots, cm
N 53-8 × Sultanina 4n	1	3	4	95
	2	11	0	175
	3	6	0	120
	4	10	0	50
Mean:		7.5	1.0	110.0
vinifera 'Hunisa'	1	113	63	130
	2	200	125	100
	3	51	74	65
	4	30	12	275
Mean:		98.5	68.5	142.5
rotundifolia 'Hunt'	1	0	0	160
	2	0	0	170
	3	0	0	65
	4	0	0	140
Mean:		0.0	0.0	133.8

N = mean numbers of nodosities per 100 cm of root
T = mean numbers of tuberosities per 100 cm of root

Of the small populations of tetraploids grown, the most significant group were those issuing from the cross N 53-8 × Sultanina 4n. These plants would be expected to have three sets of *vinifera* chromosomes and one set of *rotundifolia*, or briefly, VVVR. Four of these seedlings, at second leaf stage, were tested in 5" pots and examined 7 months after inoculation. Diploid seedlings of *vinifera* 'Hunisa' and *rotundifolia* 'Hunt' were used as controls. The roots were recorded for nodosities and tuberosities per 100 cm of root, and the results are given in Table 4. Although the number of plants in the test is small, it is evident that the tetraploid seedlings with only a single dose of *rotundifolia* genes show a high scale of resistance, as measured by root lesions. A typical example is shown in Fig. 2. This would indicate that the *rotundifolia* contribution for phylloxera resistance shows a high degree of dominance, one set of *rotundifolia* genes being sufficient to offset three sets of *vinifera* genes for susceptibility.

Field tests.

Rooted vines of the VR hybrids from the nursery were planted in a heavily infested vineyard plot at Davis in the spring of 1952, from which a dying *vinifera* planting was just removed, leaving the infested roots in place. The soil is classified as Yolo sandy loam. Irrigation was omitted during the summer. Conditions were favorable for an extremely heavy attack of the insect, as control *vinifera* rootings set at the same time failed to make any appreciable growth and some had died by

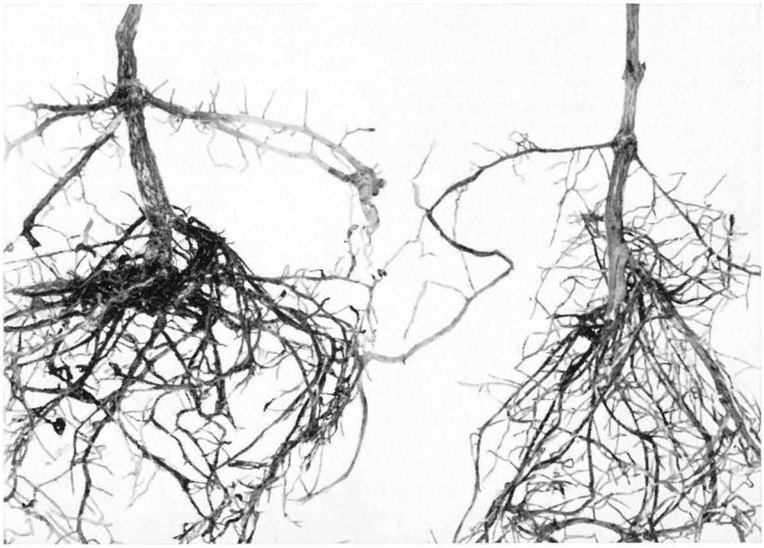

Fig. 2. A. *V. vinifera* 'Hunisa' seedling, diploid VV, extensive necrosis from phylloxera lesions (x 1,3).

B. The tetraploid, VVVR, seedling no. 3, showing considerable tolerance of the root system (x 1,3).

late summer of the second year. All of the VR hybrids made good to excellent growth.

All rootings were dug beginning Dec. 11, 1953 after two years exposure, and each was examined in the laboratory under low power binoculars (20 ×) for the presence of phylloxera and the extent of injury. Sixteen plants of each hybrid combination were included. The contrast between the hybrid and *vinifera* roots was very evident. Hybrid roots were light yellow-brown in color, the roots had smoother and less fissured surfaces, and were less branched than the *vinifera*. There were very few tuberosities or nodosities.

Live colonies with young in various stages of development were found on most plants, but considerable searching was often necesary to find them. Whereas on the *vinifera* roots the colonies were generally distributed, on the VR roots they were only established in certain widely scattered favorable areas, in the proliferating tissues of the deeper furrows in older roots, and in the crotches of the root branches. The insects were not able to lodge or multiply on the smoother intact bark of young roots. Although the *rotundifolia* vines made much less growth than hoped for, no colonies or sign of injury to the roots could be found after repeated examination.

Lodging of the phylloxera on the hybrid roots was followed by only limited development of proliferating wound tissue, with crater-like necrosis of the area, rather than the large spongy excrescences of the *vinifera* type, that is followed by general decay. The affected tissues quickly turned black. Even though colonies of the phylloxera appeared well-nourished, their presence was ineffective in producing the marked hypertorphy and hyperplasia of the *vinifera* controls. The new root growth of the hybrids was remarkably free of infection, and we failed to observe the enlarged nodosities so typical of *vinifera* root tips. The roots were thus not injured to the extent of limiting root elongation and this could be a significant factor in the hybrid's long-term tolerance.

Grafting

Grafting *vinifera* on *rotundifolia*, or the reciprocal, has never been successful. Although some unions may live for a number of years, the top growth remains very weak and stunted. Progressive weakening occurs and the end result has always been complete failure. Our results agree with RAVAZ (14), and both Hunisa and Almeria with *rotundifolia* follow the usual pattern. The only exception that we know of is the confusing report of OINOUE (9) who grafted the Italian variety Uva di Rosa on Sanrubra, a *rotundifolia* hybrid of Munson's. This "hybrid" is however pure *rotundifolia*, according to DETJEN (1919). OINOUE obtained a perfect union, it grew less vigorously at first, but by the third year was quite strong. The fruit sugared as well as on *riparia* Gloire stock. The scion became much larger than the stock.

This remains an isolated case, and the results must not have been so promising, otherwise the Japanese would have adopted the practice commercially in the warm and humid climate, where most forms of the *rotundifolia* are well adapted.

Rootstock Trials.

We were interested in determining whether the VR hybrids could be used as rootstocks and whether compatible unions were possible.

The first VR hybrids to be used as experimental rootstocks at Davis were some of the original seedling vines left in place in the field. These were the 038 series, Almeria × *rotundifolia* 1. The seedling vines were planted in June, 1950 and grafted in the spring of 1954, using a split or cleft graft at ground level. By this time the trunks were averaging about 2½" in diameter and the vines were making vigorous growth.

Five vines each were grafted to Alphonse Lavallée, Muscat of Alexandria, Molinera, and Cabernet-Sauvignon. The first three table grape varieties were chosen because they have shown more than usual difficulty in rootstock adaptability. The grafts made very vigorous growth, and unlike the *rotundifolia* root, the unions were strong and the growth remained excellent.

The fruit was harvested and examined for quality, comparing it with fruit produced on the Ganzin 1. No significant differences could be detected in color, flavor, or time of ripening for two harvest seasons. No weakening of the vines was apparent until the time the block had to be replaced in 1958.

The succes of this preliminary trial prompted a larger scale test. One block of vines established at Davis in a very fertile but lightly phylloxerated soil. Twelve VR hybrids in 10 vine lots were used as rootstock, the rooted vines were set in the spring of 1958, and field budded to Sultanina in August. The *rupestris* du Lot was used as a border vine at the ends of the 22 vine rows. The VR hybrids are listed in Table 5.

The number of vines failing to become established the first year of planting and the number of succesfully grafted (budded) vines is given in Table 5.

One can note that some rootings of VR clones do not start to grow after planting, more so than Ganzin 1 or *rupestris* du Lot. However, most all the VR vines made suficient growth for field (Yema) budding by fall and the success of budding than either of the two standard stocks. A similar experience with the same clones occurred in the plot now to be described.

Table 5

Performance of some VR rootstocks at Davis, Calif. Scion variety 'Sultanina'.

Origin	Clone	Feb. 1958 No. vines planted	June 1958 Number growing	Aug. 1958 Number budded	Aug. 1959 Number established
Almeria × *rot.* 1	037-30	10	9	9	9
	039-12	10	10	10	10
	039-16	10	10	10	10
	039-32	10	9	8	8
Hunisa × *rot.* 2	043-43	10	10	10	10
	043-52	10	9	9	8
	044-3	10	9	8	7
Hunisa × *rot.* 3	042-54	10	10	10	10
	042-58	10	9	9	7
	043-16	10	10	10	10
	043-25	10	10	10	10
	044-54	10	10	10	10
rupestris du Lot		24	24	24	22
Ganzin 1 (Aramon × *rup.*)		44	43	43	40

A second experimental block of vines was established in a cooperative trial with growers at Lodi, in the Central Valley east of San Francisco. This site is a replanted Flame Tokay vineyard. Since *vinifera* vines on their own roots continue to grow reasonably well for some years, the area does not provide a suitable short period test for phylloxera resistance. Here we again encountered some difficulty in getting a complete stand of grafted vines.

All of the Flame Tokay field budded on the VR hybrids have made excellent growth. Four rootstock selections were used, 043-43, 043-52, 043-16 and 044-54.

These same clones were used in the Sultanina trials. The performance of these varieties both as to growth, yield and quality of the fruit appears equal or superior to the Couderc 1616 and the *rupestris* du Lot in the same planting. The stocks at this age show no tendency for undergrowing or overgrowing the scion variety and are structurally strong (Fig. 3).

Discussion

The mechanisms suggested to explain resistance to phylloxera have recently been reviewed by HUSFELD (1962). He points out that the early workers were thinking of resistant vines as being those on which the phylloxera could not live, or at least not multiply to a great extent, but the present state of affairs has evolved quite differently. All of the present rootstocks now in general usage are known to produce galls on the roots and sometimes on the leaves, but are able to repair or outgrow the damage. The vines are therefore only tolerant, and hence have been also a means of spreading and perpetuating the phylloxera. Although the production of resistant vines has become a classical and indeed a most succesful instance of breeding for resistance to an insect, the job cannot said to be complete. Most will agree with PAINTER (11) that "varieties with the highest value for insect resistance

Fig. 3. Experimental rootstock trials at Lodi, Calif
Row 14. Flame Tokay on VR hybrids.
Row 15. Flame Tokay on Couderc 1616.

are those on which a specific insect is unable to maintain a population". It is only rather recently that interest in breeding for immunity has gained more attention, with the report of Becker (3) based on the earlier finding of Börner and Schilder (4) and Börner (5) that *Vitis cinerea* 'Arnold' is immune to phylloxera. Anders (1) has expressed doubts about using a species as distantly related or as untried as *cinerea* Arnold, feeling that it may introduce undesirable characteristics into the hybrid. This argument should apply even more so to *rotundifolia,* which is often considered as a taxonomically separate genus, *Muscadinia* Small. However, it seems the only way to resolve whether certain unfavorable genetic linkages may exist with the immunity or high resistance is to continue the breeding tests. In view of the fact that the *rotundifolia* carries many desirable factors for resistance to other insects and diseases seem to make it worthwhile to explore its possibilities. The high resistance and practical immunity of some of the VR hybrids, their initial success as rootstocks, lend encouragement to this quest.

There are advantages in having vines "immune", in the sense that the insect cannot injure the vine or reproduce on it under any known conditions. First of all, it would speed up the seedling selection of resistant vines, as an "all or none" separation can be made. Next, it would eliminate altogether the extremely long testing periods in the field necessary to established the practical sufficiency of the resistance in only tolerant vines, a costly and sometimes in the end a disastrous procedure. It is only necessary to recall the failures of innumerable varieties at one time recommended as highly resistant. It would eliminate the possibility of biological races of phylloxera developing by mutation and selection that might be capable of more seriously damaging tolerant vines that were previously of a satisfactory scale of resistance. Since the *rotundifolia* is recognized as the grape species most highly resistant, to the point of immunity, it is a most promising parent to test the "immunity" idea. In the VR hybrids described herein, some vines even in the first generation appear immune. However, further techniques must be developed to conclusively demonstrate such immunity under a wider range of environmental conditions. For rootstock purposes, a wider range of hybrids with other *Vitis* species is possible with the *rotundifolia*. However, many of the VR hybrids, having half *vinifera* parentage are much more resistant than the known first generation hybrids of *vinifera* with other species such as *riparia* or *rupestris*, thus indicating the greater potency of *rotundifolia* in transmitting resistance.

The dominance of *rotundifolia* genes for phylloxera resistance vs. the susceptibility of *vinifera* has been demonstrated in tetraploid hybrids, where a single dose out of four is sufficient to produce a plant of considerable tolerance.

Although the limited number of plants available did not permit the parallel testing of the same VR hybrid clones to all five collections of phylloxera in one and the same experiment, certain comparisons made, such as the Alexander Valley vs. Exeter collection in the tank experiments show no evidence for different biological races of the phylloxera in California. Certain clones however were used in different experiments and hence exposed to all collections. Clone 043-13 proved highly susceptible to lesion formation in tank, pot, and field experiments with all collections of phylloxera, whereas 043-15 occasionally produced small nodosities, but no tuberosities large enough to be observed.

The VR hybrids as a group present certain disadvantages from the propagation standpoint. The mother plants do not produce abundant cutting wood until they are four or five years old. The cuttings are thin and not as straight or as easily handled as most species. The wood is harder and more difficult to prune. The field nursery stand of 200 clones tested over several years has varied from 0 to 95%. It is therefore possible to select clones that will root quite satisfactorily. A danger here might be that in selecting good rooting ability we might also lose the high phylloxera resistance if these characteristics are closely linked. The stand of vines after planting is somewhat lower than most rootstocks and the vines are slower in resuming growth and are slightly more difficult to graft. These apparent difficulties may be resolved in the development of special training and handling methods. On the favorable side, the stocks rarely sucker and do not need to be disbudded before planting. However unless VR stocks can be selected that show considerable long term adventages over those now used, these presumably minor difficulties in propagation might be severe hindrances in their commercial adoption.

Although *rotundifolia* and *vinifera* cannot be grafted inter se to be of practical use, all the VR hybrids clones tested thus far with seven *vinifera* varieties have given satisfactory unions and have produced vigorous and fruitful plants. None of these tests have yet reached more than eight years of age, hence we must keep in mind that the tests are only preliminary. However the stage is set to plan for more extensive trial of this type of hybrid, and to use it further in gene transfer into the *vinifera* grape.

Summary

1. In greenhouse and field tests of rooted vines and seedlings, a considerable number of *vinifera* $\times$ *rotundifolia* F_1 hybrid clones exhibit high tolerance or immunity to the root form of phylloxera, as judged by the formation of lesions or the insects found lodged on the roots.

2. The formation of root lesions is related to the anatomical structure, the more closely it resembles the *rotundifolia*, the fewer and smaller the lesions.
3. Phylloxera samples from five different areas in California have not been found to differ in gross morphology or in their reaction to the VR hybrids.
4. The species *rotundifolia* contributes genes exhibiting considerable dominance for resistance in the F_1 generation.
5. Unlike the *rotundifolia* parent, the VR hybrids can be successfully used as rootstocks for *vinifera* grapes, although observations are only for eight years and hence preliminary.
6. Although the VR hybrids are less easy to propagate than many common rootstocks, the variation is great enough between clones to permit selection.

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