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0014-4754/86/080914-08$1.50 + 0.20/0

The potential role of (*vinifera* × *rotundifolia*) hybrids in grape variety improvement

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Key words. Grape; breeding; pest resistance; *vinifera-rotundifolia.*

Introduction

The objective of this review is to present some examples of work in progress that emphasizes the great potential of using the gene resources of the *Vitis rotundifolia* (now *Muscadinia rotundifolia* Small) as a donor to introduce resistance or immunity to a wide range of pests that cause extensive loss in yield and quality of the *vinifera* grape. Examples cover a whole range of organisms; fungi, bacteria, insects, nematodes and, most important, soil borne viruses causing vine degeneration. The reciprocal approach to introduce the high fruit quality of the *vinifera* has been hindered by the lack of cross compatibility when *rotundifolia* is used as the female parent.

The vinifera grape[27]

The *vinifera* grape, still found in the wild state as isolated relic populations around the Mediterranean Basin and the Middle East, is the most renowned of all the species in the genus *Vitis* because of the excellent quality of its fresh or processed fruit. The wide variation in morphological characters suggest an origin from a complex of subspecies. *Vinifera* has given rise to an immense number of cultivars. The wild plant, as found in the forests, produced edible and palatable fruit. Domestication was uncomplicated, only sparing and protecting the most desirable vines in place was necessary.

The fruit qualities that make the *vinifera* a standard of excellence are the thin and tender skin closely adherent to the firm and meaty pulp; large berries, some seedlessness, attractiveness in color and form, high yield of clear juice, high sugar content, medium to low acidity, low phenolics, low pH, mild or subdued flavors, large and well-filled clusters with good adherence of the berry. The importance of any one of these characteristics vary with vineyard site and the intended use of the product. For wine grapes to be harvested mechanically, good adherence of the berries is a negative factor, but for table grapes to be shipped and stored it is a positive factor. High sugar content, though generally desirable, is not sought for champagne-type wines.

Propagation of the better ones and increase were relatively easy, as this vine propagates readily by cutting segments of mature canes (cuttings) derived from the current season's growth and burying them in soil in furrows in an upright position, leaving the uppermost bud exposed to begin growth in the spring.

From its ancestral home in the Middle East, about 4000 B.C., cultivated varieties began spreading to the east and west. The main commercial development centered around the Mediterranean Basin. The *vinifera* vine was introduced into the New World via Spanish and Portuguese conquest. North America, in contrast to Middle Asia, has an abundance of wild grapes, over 23 species are recognized. The *vinifera* grape introduced by the colonists along the Atlantic coastal plain had great difficulty in surviving in what was thought to be a grape paradise. Winter temperatures were too low and the vine was relegated to greenhouses or against walls. The phylloxera, an aphid insect, attacked the root system. Fungus diseases were very damaging in the rainy summer period. Efforts to make *vinifera* succeed were hopeless, but eventually spontaneous seedlings arose that were hybrids of the American wild vines and the few pampered *vinifera*. Such varieties as Concord, Alexander, and Isabella are examples. These became known as American hybrids and proved much better adapted than *vinifera*.

Catastrophe befell the heretofore tranquil and remunerative *vinifera* vineyards of Europe when, perhaps mostly out of curiosity, some American vines were introduced from the colonists. New and very destructive immigrants arrived that in turn decimated the vineyards of Europe and eventually became worldwide, wherever *vinifera* was grown. These scourges were powdery mildew in 1845, phylloxera in 1865, downy mildew in 1878, and black rot in 1885. Phylloxera was the pest that defied any chemical control, and the French government undertook a study and search of the American wild vines countrywide to discover and import resistant vines. This proved successful and eventually the dying vineyards were removed and the fruiting varieties reestablished on vines (rootstocks) whose roots were resistant. What were once individual vines became a two story component.

The rotundifolia grape

In the catalogue of North American wild grapes, the *rotundifolia* should receive the special attention of the breeder. Formerly considered a *Vitis*, it is now recognized as a member of the genus *Muscadinia* (Small), characterized by 40 somatic chromosomes instead of the 38 of *Vitis*. Great differences in morphology and anatomy are evident. Our theme has to do mostly with pest resistance. Viala[33] mentioned that *rotundifolia* was the most resistant of the wild vines to fungus diseases.

Rotundifolia is native to the southeastern United States, where the climate is warm, rainy and humid during most of the year. It is most abundant in the states bordering the Gulf of Mexico, reaching to the southern half of Florida, the eastern half of Texas, and northward to the Arkansas border. Its favorite habitats are the low coastal plains along the Atlantic from Virginia southward.

In its natural environment, *rotundifolia* has the largest berries of any known grape species, equal to some of the table grape cultivars of *vinifera*. The shape of the berry is spherical or only slightly ovoid, in contrast to the more elongated forms found in cultivated *vinifera*. The skin is thick and leathery in texture and is very resistant to cracking. The whitish pulp of the berry is mucilaginous or slimy and separates from the skin as a glob, with the seed clinging inside.

The fruit clusters are globular in shape and have few berries that are uniform and well spaced. They ripen sequentially and the force to remove them correlates with the degree of maturity, and selective harvest is possible[2]. Some *vinifera* varieties deteriorate rapidly if rains occur during the ripening season. In South Africa, Wagener[34] reported severe bunch rot in 'Chenin blanc'. Of the spoiled clusters, 50% had infections of *Botrytis cinerea*, 25% with *Aspergillus* and 10% *Penicillium* as well as unidentified bacteria. If the grapes are not processed quickly, less than one hour after harvest, no more than 50% spoiled clusters can be used without compromising wine quality. Under similar conditions in the southeast U.S., cultivated *rotundifolia* would be unblemished.

The most remarkable features of the *rotundifolia* vine are its longevity and resistance to the diseases and insects that make the widespread culture of the *vinifera* vine uneconomic or impossible. A few examples must be convincing that this species carries the gene resources that are almost entirely absent in *vinifera*. Most of these genes have a high degree of dominance and the F^1 hybrid often illustrates this fact.

Progress in gene transfer was long delayed due to the complete chromosomal sterility in the first populations of F^1 hybrids, terminating early efforts to breed advanced generations. Nonetheless such sterile plants are being tested increasingly as rootstocks. In the use of these as rootstocks, some difficulties in propagation have arisen. *Rotundifolia* roots with great difficulty from dormant woody cuttings. Even under greenhouse conditions only one in a thousand produces a usable rooting. Rooting of the VR hybrids ranges from 0 to 40% in commercial field nursery plots. Like *rotundifolia*, green leafy cuttings made in the summer root very readily and can be grown in containers for field planting.

Modern cultivars produced by breeders in some of the southern U.S. are much improved over the native forms, particularly in berry size, sugar content and general quality[18]. The berry size of some recent cultivars varied from 4.9 to 9.3 g. The clusters are small, globular and have few berries, averaging 5.3 to 7.1. The sugar content of newer selections now approach *vinifera* varieties, as do the total yields (table 1).

Yields have been increased remarkably and are much more dependable, since most new varieties have hermaphroditic flowers and do not require interplanting with male vines to insure cross pollination. Like the *vinifera* grape, the female vines are pollen sterile and are very useful in breeding programs. The *rotundifolia* is one of the latest vines to commence growth and therefore offers more security against spring frosts. However, the season

Table 1. Evaluation of 5 muscadine grape cultivars at Experiment, Georgia. (Values represent means of 5 years) (from Lane[18])

Cultivar	Berry size (g)	No. berries per bunch	Soluble solids (%)	Dry stem scar^z (%)	Yield (MT/ha)
Carlos	4.9	7.1	14.7	87	12.1 a^y
Fry	9.3	5.3	17.9	56	10.6 ab
Higgins	8.6	6.0	15.3	46	11.4 a
Magnolia	5.2	7.9	16.6	53	9.3 b
Summit	8.8	6.3	20.5	84	10.1 ab

^{z}Percentage of berries not torn at point of detachment from pedicel.
^{y}Means separation by Duncan's multiple range test, 5% level.

of fruit maturity is correspondingly later, exposing the fruit to fall rains.

An interesting and desirable attribute is the progressive ripening of the berries which would enable selective harvesting. On some cultivars, the berries separate cleanly from the pedicel, and the berry is entirely sealed. Since no juice is released, fruit spoilage is minimized. Mechanical harvesting is easily performed by a trunk shaker and catching frames. Although cultivars differ in their suitability for mechanical harvest[2], the inheritance of this characteristic is unknown and has not as yet been transferred to the *vinifera* grape.

In contrast to *vinifera*, *rotundifolia* vine structure offers much less opportunity for the invasion of destructive organisms. The leaves are very shiny and varnished with a protective coating of wax, which repels fungus establishment. The canes are very slender and have a densely packed woody cylinder. The pithy core is much smaller and is continuous, without the enlarged diaphragm and nodes of *vinifera*. Pruning wounds are thus smaller and offer less access to organisms that cause deterioration of the core of the vine trunk and its arms. Thus *Eutypa armeniacae*, a fungus gaining entrance through pruning wounds, produces cankers that eventually cause dead arm, preceded by symptoms of spindly and delayed shoot growth, very small leaves and distorted and unfruitful inflorescences. This disease of cosmopolitan distribution has not been reported to invade *rotundifolia*. No symptoms of the disease have appeared in old plantings of VR hybrids located adjacent to a variety collection of *vinifera* planted in the 1950's, now with over 80% having symptoms.

The long shreds of bark separate and remain attached to the *vinifera* vine affording a haven for the protection and hibernation of crawling insects such as mealy bug, mites, cutworms, etc. The tight seal of the *rotundifolia* offers fewer such havens.

Of the many native species of grapevine, the *rotundifolia* is the most unique and offers the greatest potential as a gene donor to introduce disease and pest resistance into cultivated varieties.

The hot dry year of 1980 in North Carolina produced a very high pH in the *vinifera* 'Gewürztraminer', 'White Riesling' and 'Chardonnay', whereas the *rotundifolia* cultivars 'Magnolia', 'Carlos' and 'Noble' were characterized by low pH and good acidity, but were much lower in soluble solids (table 2). Addition of sugar to the must is mandatory in producing dry table wines in the southeastern states.

In California, experimental wines have been produced in the late 1960's from vigorous and high yielding vines resulting from backcrossing the F^1 VR hybrids to different *vinifera* wine grapes. The composition and quality of several of these musts and wines were of *vinifera* type.

Table 2. Average analysis of juice for four years of three cultivars, 1966–69

	Soluble solids	Total acid (g/100 ml)	pH
Carlos	14.4	0.78	3.20
Magnolia	14.7	0.61	3.35
Scuppernong	14.8	0.84	3.12

Source of data, Nesbitt et al.[25].

Rotundifolia has flavoring compounds not generally present in *vinifera* and new profiles could be added to our present wine varieties[28].

Cytogenetics of the F^1 VR hybrid

The F^1 hybrid of *vinifera*♀ × *rotundifolia*♂ is easily accomplished, but succeeds only rarely when *rotundifolia* serves as female[35]. The hybrid has 39 somatic chromosomes, 19 derived from *vinifera* (2n = 38) and 20 from *rotundifolia* (2n = 40)[30]. The hybrid is highly sterile and completely unfruitful, but the *vinifera* parent chosen may result in the hybrid producing a few viable seeds[14]. Doubling the chromosome number of the sterile hybrid reduces plant vigor and some sterility remains[15].

Hybrid sterility is chromosomal. Maximum pairing usually centers about 13 II + 13 I at the first metaphase of meiosis. This has been interpreted[30] as representing 13 chromosomes of *rotundifolia* as homologous with the *vinifera* set, the bivalents can be represented as $13R^RR^v$. The 13 unpaired chromosomes represent two basic genosomes of different unknown ancestral species 6A+7B. *Vitis* is therefore a secondary polyploid, a hexaploid of three ancestral species, R^R+R^v+A and *Muscadinia* R^RR^v+B. Diploidization has proceeded to produce normal bivalent pairing in each genus.

Lavie[19] has reported some tropical genera of the family to have 2n = 22 chromosomes, from which one might guess there are three basic chromosome numbers 5, 6 and 7.

Pierce's Disease

Pierce's Disease, first recognized as 'Anaheim Disease' and 'California Vine Disease' is the most deadly of all vine plagues; even vigorous and well established *vinifera* vines cannot survive more than three or four years after infection. No practical method of control or attenuation of the disease has been possible, so that once a planting succumbs, the area is virtually sterilized for future plantings of *vinifera* or most of its hybrids. At one time thought to be a virus, the organism has been identified as bacterial. The principal vector is the blue-green sharpshooter, *Carniocephala*, which is abundant on many host plants in the coastal vineyard regions of California. The disease prevents the culture of the *vinifera* grape in the southeast and those areas bordering the Gulf of Mexico, including much of Texas and parts of Mexico. Breeding of resistant varieties has been pursued by Mortensen using resistant species native to Florida.

VR hybrids in the F^1 generation have been tested since the 1940's at the Los Angeles campus of the University of California, in an endemic area of the disease. Over 200 wine varieties of *vinifera* have proven highly susceptible and succumb within 2-3 years. Sterile VR hybrids survive and show no symptoms. Advanced generations are being grown and tested for resistance in Napa County, California.

Powdery mildew

Powdery mildew, *Uncinula necator* (Schw.) Burr. is cosmopolitan in distribution and attacks the *vinifera* vine in all climatic zones, from the temperate to the tropics.

Although there is considerable variation between varieties in susceptibility, all varieties require preventive treatment. All green parts of the vine may be infected, but the loss of crop is dreaded most. *Rotundifolia* and the hybrids of it are highly resistant. Some of the newly bred cultivars of *rotundifolia* may show occasional russeting of the fruit, but without any reduction in yield or fruit quality.

A breeding program to transfer the resistance of *rotundifolia* to *vinifera*[32] was started many years ago by repeated backcrossing to *vinifera* with selection for high resistance at each generation. Seedlings were first inoculated in the greenhouse and the most resistant ones transferred for vineyard tests. *Vinifera*-type vines homozygous for mildew resistance have been isolated. Some irregularity in chromosome pairing suggests that a considerable block of a *rotundifolia* chromosome has been transferred.

Powdery mildew growing on the surface of the fruit causes physiological changes that markedly reduce wine quality, even though the berries are not ruptured[29]. At Davis, California, mildewed samples had higher total acidity in the grapes but lower acidity in the wines, with slightly higher sugar content (Brix) than the controls. Although fermentation rates were similar, the wines from mildewed samples browned excessively. Taste panels found the mildewed wines bitter and off-taste. The fungus on young leaves distorts the growth and reduces normal function. Most of the seasonal damage and reduction of yield is initiated by the berries splitting open, because of the differential ripening. Surface areas of the skin infected by mildew are delayed in ripening and provoke unequal osmotic pressures in the berry flesh. As juice is released from the cracked fruit, invasion by other organisms brings about extensive spoilage.

Phylloxera

The complete sterility and failure of the F^1 hybrids to produce fruit led us to explore other avenues in which these vigorous and resistant vines could be utilized. Could they be used as phylloxera resistant rootstocks? The traditional method to produce rooted vines is by cutting segments 12–15″ long of the mature and dormant canes and planting them in a nursery. Using this method, the *rotundifolia* cuttings fail to root and, even if placed in a greenhouse, about one in a thousand survive. The commercial propagation of *rotundifolia* uses a system of

Figure 1. *Muscadinia rotundifolia.*

Figure 2. Infectious degeneration in vineyard, Narbonne, France.

stooling or layering, mounding soil over the canes while they are still attached and nourished by the mother plant for one growing season. Green cuttings of the summer growth with the leaves attached can be treated with growth regulators and rooted more rapidly and easily.

Propagation of vines, to serve as the root system of a fruiting variety, begins with the dormant pruning of the current season's growth. The canes are cut up into segments of 12–16″ in length and planted upright in a nursery row. With few exceptions each rootstock variety is a clone, derived from the vegetative reproduction (cuttings) of an original selected plant having the desired resistance or aptitudes not available in the cultivated variety.

Tests carried out in 1957 and subsequent years showed the VR hybrids to have high resistance and in some cases immunity to the root form *(radicicola)*[10]. Since the relative resistance of commercial rootstocks is influenced by environmental factors as well as the extent of necrosis caused by the insect, a long time span is often necessary to guarantee adequate field performance. Thus in Sicily preliminary experience with the *vinifera* × *rupestris* Ganzin 1 was so promising that virtually the whole vineyard acreage was reestablished on this root, only to fail after a few seasons.

The affinity between the rootstock and fruiting top signifies the relationship between the two systems. Affinity or lack of it may be due to anatomical differences, usually first expressed at the line of graft union. Grafting *vinifera* on *rotundifolia* or the reciprocal is incompatible and lacks affinity. Some weak growth may occur, but the union is unsatisfactory. On the other hand, some *rotundifolia* clones can be grafted successfully on hybrid rootstocks, such as *vinifera* × *rupestris* hybrids. VR hybrid rootstocks were first used on several table grape varieties and formed satisfactory and permanent unions. Several rows of VR clones were field grafted to Flame Tokay, one of the most vigorous varieties in commercial use, with very good results.

A previously unselected population of 278 offspring generated from 26 parents involving *vinifera* – *rotundifolia* hybrids yielded some segregants that carried immunity to phylloxera. Although the fruit is of *vinifera* quality, further selection is needed to obtain commercially acceptable varieties[11].

Anthracnose

Anthracnose (*Elsinoe ampelina* de By Shear) is a very damaging disease in tropical viticultural areas with a humid, warm and rainy growing season, resulting in lesions destroying leaves, shoots and fruit. All *vinifera* varieties tested in Florida by Mortensen[23] were highly susceptible; whereas, cultivars of *rotundifolia* were devoid of any symptoms. Reaction of the VR hybrids has not been investigated.

Nematodes

Rootknot nematodes of the genus *Meloidogyne* (Goeldi) Chitwood are considered a limiting factor in viticulture, especially in warm climates and sandy soils. Nurseries and replanting situations are often problem areas. Even the most extensively used commercial rootstocks derived from *Vitis* species or hybrids serve as hosts for some populations of *Meloidogyne*. Lider[20] screened a number of American species for resistance to the common form *M. incognita acrita* Chitwood, a single dominant gene conferring resistance. Resistance of container-grown vines to the three species *incognita, arenaria* and *javanica* was investigated by Bloodworth et al.[4].

Resistance was assessed by determining the increase in nematode number after single inoculations and measuring shoot growth four months after beginning the experiment. There were no detectable galls or populations of the three nematode species on *rotundifolia* cultivars, agreeing with earlier reports of high resistance or immunity. Shoot growth showed no relationship to the inoculation concentration.

With few exceptions, the F^1 VR hybrids showed no galling and were ranked resistant.

An unselected population of 807 offspring of 46 families representing VR hybrids backcrossed to *vinifera* and the F^2 progeny of these were rated as resistant = 1, to very susceptible = 4 in reaction to *M. incognita acrita*. Heritability was estimated by parent-offspring correlation to be 0.391 = 0.06. Relatively rapid genetic gain is to be expected in the population based on their own performance and subsequent mating inter se. Many of these resistant selections are of *vinifera* type, but further improvement in fruit quality for table grape use is needed[12].

The nematodes *Xiphinema index* and *Longidorus* have received greater attention in the last few years, since the discovery that they not only attack vine roots but are vectors of virus. These are discussed more at length under virus diseases.

Virus diseases

The most serious unresolved challenge in modern viticulture is the increasing loss of yield and fruit quality caused by virus infected soils. It is a problem that has become increasingly severe with time. It is in the most renowned appellation vineyards where the question is now one of survival. Infectious degeneration of the vine wreaks its havoc slowly, and at first almost imperceptively, so that growers are often unaware of what has finally brought them to the brink of abandonment of their historic and irreplaceable vineyard sites. (See photo on infectious degeneration, Narbonne, France).

Figure 3. Fruit cluster of *rotundifolia*.

Infectious degeneration

The most damaging and widespread viruses in grapevines[9] belong to the group called Nepovirus, 'Ne' representing transmission by nematodes that live in the soil and 'Po' the polyhedral shape typical of the virus particle. The most common virus complex is called fanleaf, from the deformation of the leaf outline and opening out of the petiolar sinus to resemble the base of an open fan. The course of the disease is slow but irreversible, deformation of leaves, shorter and irregular internode spacing of the shoots (court noué) eventually weak and erratic shoot growth with increasing failure to set fruit. The yellowing mosaic of the leaves of irregular pattern is the most striking symptom. Two groups of nematodes are vectors, *Xiphinema* and *Longidorus;* the first the most important and widespread. No control methods have proven practical, as clean vines planted in infected soil soon contract the disease. Soil fumigation has not afforded long term protection and is very expensive.

The solution appears to rest in breeding vines whose root systems are resistant to the nematode vectors or are resistant to the virus itself. A rootstock combining both types of protection would be even a more acceptable solution. By 1983, some California workers[31] concluded that soil fumigation was the only effective control measure for grapevine fanleaf virus. They suggested that with nematicidal fumigants, replanting of diseased vineyards could be scheduled every 15–20 years and still be successful economically. The development of a rootstock with multigenic resistance was being explored.

Screening of a number of *Vitis* species and clones to determine the pattern of inheritance of resistance to *Xiphinema* by Meredith et al.[21] theorized a dominant gene and two recessive genes. Difficulties in classifying the degree of resistance were pointed out. In one case, the same species (solonis = longii) were recorded as both resistant and susceptible. An earlier screening test in 1968 by Kunde et al.[17] led to the use of *rufotomentosa* as a possible parent in breeding for resistance.

In France, Bouquet[5] and his colleagues at Bordeaux took up the challenge 'to obtain new rootstock varieties with complete resistance to phylloxera and root-knot nematodes, in contrast to the usual rootstocks which are only tolerant. The main objective is to incorporate in these new varieties a high field resistance to the transmission of grape fanleaf virus by its vector, the dagger nematode *Xiphinema index.'*

He demonstrated that *rotundifolia* when shoot-tip grafted on virus infected vines were resistant[6] and that no virus transmission could be effected with viruliferous dagger nematodes[7]. The ELISA test coming into general use for detecting and assaying plant viruses was recommended as a rapid selection method[8].

Rotundifolia cultivars are remarkably free of virus. They are resistant to the principal vector of GFL virus. A large collection of F^1 hybrids of *vinifera* × *rotundifolia* were screened for resistance to *Xiphinema index* in our greenhouse in 1967.

Cuttings were first rooted in sterilized soil and then potted in duplicate tests. After one year, 200 g of soil was removed and washed for extraction and counts of nematodes. The roots were washed clean, weighed and the nematode damage noted visually. Resistance varied from the resistant *rotundifolia* to the very susceptible *vinifera* parents Hunisa and Almeria. No complete classification of the total progeny was possible because many plants failed to produce root systems extensive enough to judge the degree of infection. The plants with highest resistance have been propagated for increase and field trials.

Some of these selections previously rated for high resistance or immunity to phylloxera have been planted in vineyards with severe degeneration by Lider and Goheen, who have reported results of these initial trials at the Fourth Int. Grape Breeding Congress, Verona, April 1985 (in press). Two rootstock varieties have demonstrated excellent growth and yield of Cabernet Sauvignon scions and are being patented by the Regents of the University of California.

For the production of even more desirable rootstocks, the potential of using *rotundifolia* in hybridization with other species of *Vitis* needs to be explored. For example, it is likely that the VR rootstocks will not be adapted to highly calcereous soils typical of many viticultural regions, such as Champagne and Cognac. Greater ease of propagation may be introduced via *riparia,* which could contribute a shorter growth cycle and more winter hardiness. Although interspecific hybrids within the genus *Vitis* are vigorous and fertile, some exceptional results have been noted in intergeneric crosses. *Vitis champini* × *Muscadinia rotundifolia* has generated very weak and useless plants, in contrast to the uniformly vigorous VR hybrids.

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