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The heritability of resistance to root-knot nematode (*Meloidogyne incognita acrita* CHIT.) in *Vitis vinifera* × *V. rotundifolia* hybrid derivatives[1])

by

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Die Heritabilität der Resistenz gegen Wurzelgallennematoden (*Meloidogyne incognita acrita* CHIT.) bei *Vitis-vinifera* × *V.-rotundifolia*-Kreuzungsnachkommen

Zusammenfassung. — Eine Population von 807 Nachkommen aus 46 Familien, die aus Kreuzungen zwischen 26 Eltern (Quasi-F_1-Kreuzungen aus *Vitis vinifera* und *V. rotundifolia*) hervorgegangen sind, die Eltern selbst, 12 *V.-vinifera* × *V.-rotundifolia*-Kreuzungen (VR) sowie Muskat von Alexandria und Dogridge als Kontrollen wurden in einer Rebanlage der Universität von Kalifornien, Davis, herangezogen und im Gewächshaus auf ihre Resistenz gegen das endoparasitische Wurzelgallenälchen *Meloidogyne incognita acrita* CHIT. geprüft. Verschiedene Sämlinge und Eltern sowie fast alle VR-Kreuzungen zeigten Nematodenresistenz; die Ergebnisse wurden durch eine zweite Resistenzprüfung bestätigt.

Die Heritabilität wurde auf 0,391 ± 0,06 geschätzt. Die durchschnittlich zu erwartende Verbesserung der Resistenz in der Nachkommenschaft aus zufällig gekreuzten Eltern, die unter den oberen 5 % ihrer Generation rangierten, wurde errechnet. Das Ergebnis zeigt, daß eine relativ rasche genetische Verbesserung erwartet werden kann, wenn sich die Reben einer leistungsfähigen Population zufällig untereinander kreuzen können. Aufwendigere Methoden der Sämlingsprüfung und der Inzucht, durch welche üblicherweise die nichtadditiven Anteile der genetischen Variabilität ausgenützt werden, erübrigen sich dann.

Die Verwendung der resistenten Reben als Unterlagen und, längerfristig, zur Kombination von Resistenz und wünschenswerten Eigenschaften der Trauben werden diskutiert.

Introduction

Plant parasitic nematodes are recognized today as important destructive pests of all common cultivars of *Vitis vinifera* (20). Of these nematodes, the root-knot group (*Meloidogyne* spp.) are probably the most widely spread and of the greatest economic importance to the grape industry in California (20 and 24). Differences in cultivar susceptibility have been reported but are not significant enough to provide a solution within *V. vinifera*.

Although rootstocks resistant to the root-knot nematode, *M. incognita acrita* CHIT., have been reported by SNYDER (26) and LIDER (16, 19 and 20), obtention of resistant vines with desirable fruit characters has not been attempted, and growers have had to use expensive grafting techniques to propagate their vines in infected areas. Still the reaction of the fruiting varieties grafted to the available resistant stocks has not been entirely satisfactory (18).

The objective of this study was to establish the feasibility of incorporating root-knot nematode resistance into grape cultivars in order to eliminate eventually the high cost of grafting these cultivars to resistant rootstocks. In the short term, resistant

1) Portion of a thesis submitted by the senior author for the Ph. D. in Genetics.

stocks with *V. vinifera*-like phenotype and easy to propagate might solve the problem of lack of compatability and increase fruit quality.

The literature on genetics of inheritance of root-knot nematode resistance in grapes is limited. The only work is that of LIDER (18) who studied the inheritance of resistance to root-knot nematode, *Meloidogyne incognita acrita* CHIT. He concluded the following: some species such as *V. vinifera* and *V. labrusca* have one recessive gene for susceptibility (e.g. nn), other species such as *V. champini* and *V. candicans* carry a dominant homozygous or heterozygous gene for resistance (e.g. NN or Nn), still other species, including *V. rupestris,* have two genes (e.g. Nn, Rr) in which one gene, i.e. R, suppresses the expression of the other, N, thus providing a situation where the susceptible *V. rupestris* could contribute resistance to a portion of its offspring when crossed to susceptible plants. In a native population of *V. solonis* OLMO (23) showed that there was marked difference between clones in their ability to transmit resistance.

BARRONS (2), in his studies on inheritance of resistance to root-knot nematodes in beans, concluded that there are two dominant genes for susceptibility. WATTS (27), in his study on tomatoes, in crossing *Lycopersicon peruvianum* and *L. esculentum* resistant and susceptible to the root-knot nematode, respectively, concluded that resistance is conditioned by two dominant genes. FATUNLA, and SALU (9) concluded the same thing in tomatoes and that the dominance is incomplete. BOQUET (5) by using reciprocal crosses between resistant and susceptible varieties of soybean, concluded that resistance is governed by one major gene with one modifier gene. SCHWEPPNHAUSER (25), studied the inheritance of resistance to the root-knot nematode in *Nicotiana longiflora* and found that resistance is conditioned with a single dominant gene with at least one linked modifier.

We designed an experiment to establish how it is inherited in *V. vinifera* × *V. rotundifolia* hybrid derivatives, namely to obtain an objective quantitative estimate of the rate that resistance in the offspring can be increased.

Materials and methods

The population studied consisted of 26 parents and 807 genotypes of the 46 families generated by crosses. Parents were quasi-F_1 hybrids of *V. vinifera* × *V. rotundifolia,* i.e., the e and F series generated by OLMO (22). They were planted on their own roots in the vineyard of the University of California, Davis, as part of the grape breeding program of the University. Sibs within progenies were planted adjacently in progeny rows.

Green cuttings were taken from the plants in the vineyard during early summer and rooted in a greenhouse. At least 2 cuttings from each offspring (permitting 2 randomized blocks to be used) and 5 cuttings from each parent as well as 60 cuttings of Muscat of Alexandria and Dog Ridge were used as controls (susceptible and resistant cultivars, respectively). The rooted cuttings were then transplanted into steam-sterilized, light sandy soil in two tanks. The tanks, 44″ × 96″ and 72″ × 142″, with only 6" depth each, gave much quicker build up and infestation . They were equipped with a sloping bottom and the drainage water was collected from a 3/4″ spout and emptied into a bottle. 3 wks after transplanting the soil was well inoculated with the nemotodes which had been built up on tomato roots (variety California VF36, a very susceptible tomato). The soil was irrigated regularly and the plants were sprayed for pests and were fertilized as needed.

15 wks after inoculation, by which time there was heavy damage to the susceptible controls, the plants were rated for resistance from "1" to "4", "1" being the most resistant and "4" being the most susceptible (OLMO, unpublished data):

1 = No galling, no apparent root injury.
2 = A few small and occasional galls on fibrous roots.
3 = General galling of main and large roots, but growth of fibrous roots not badly restricted.
4 = Heavy galling of whole root system, fibrous roots matted, partly decayed, length growth severly restricted (Figs. 1 and 2).

All the plants given a rating of "1" were replanted in the heavily infected soil to be retested. After 5 months they were scored again for resistance.

Heritability was estimated from the linear regression of individual offspring performance records on the average performance of their parents, the mid-parents performance being repeated within progenies (4).

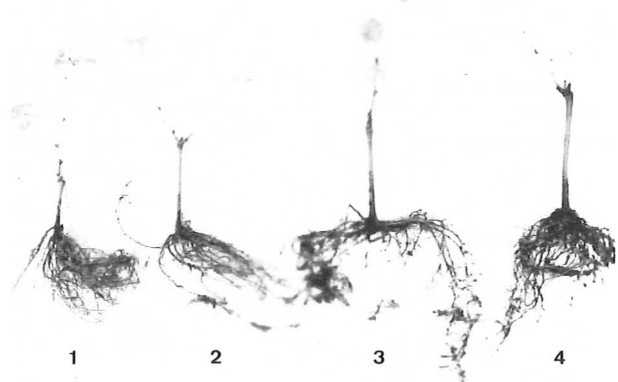

Figure 1: Seedlings rated "1" (uninfected) to "4" (heavily infected).
Sämlinge der Resistenzklassen 1 (nichtbefallen) bis 4 (stark befallen).

Results and discussion

In the study of resistance to the sedentary endoparasitic root-knot nematode, it was possible to assign degrees of resistance to the nematode possessed by different plant genotypes. All the susceptible control plants scored as "4" except a few as "3" and all resistant controls as "1", indicating that tanks were equally inoculated and infected. Table 1 shows the degrees of resistance to the nematode possessed by parents (e, F, P and T series), VR hybrids (0 series) and some of the seedlings. Generally, *V. vinifera* is very susceptible and *V. rotundifolia* is tolerant to this nematode (3, 18 and 22) and even its shoot growth is not affected (3). Many of the VR hybrids showed resistance; this result is in favor of resistance dominating over susceptibility which already has been shown in other hybrids (18 and 22). The parents showed different degrees of resistance. The reason for this observation is that the parents have been derived from different

Figure 2: Seedlings rated "1" and "4".
Sämlinge der Klassen 1 und 4.

sources. A number of them have *V. rotundifolia* genes in their backgrounds (3 and 22), so they generally showed higher degrees of resistance than others. The degrees of resistance for all seedlings are not shown here, since 807 seedlings were tested. They also showed different degrees of resistance, since they had been derived from highly heterozygous and diversified sources.

Since the immune plants were needed for later improvement programs, they were retested to be sure of their immunity. Many of them still scored "1" (Table 1). Many were rated "2", which still might be genetically immune, since the population of nematodes was very high and very few plants were left in the tanks. Approximately 2,000 plants were used originally. When a population of pests is too abundant, they have to attack whatever plants are left so even immune plants would be attacked but still remain tolerant (Raski, personal communication). 4 out of 10 resistant controls scored as "2" which also is in favor of the above statement.

A few of the retested plants showed a score of "3". These are considered as susceptible. The reasons that they were rated as "1" in the original test are probably as follows:

1. Some exceptional areas in the tanks could have escaped infection, even though the control plants distributed over the whole areas were attacked, or
2. These plants had been infected by the nematodes, but apparently no injurious root damage was apparent because of the short time interval.

The results of heritability studies are summarized in Table 2. Parents were classified according to the mean of their performance. The body of the table represents the distribution of progenies.

Table 1

Parents, VR hybrids and seedlings and their degrees of resistance (e, F, P, and T series = parents; 0 series = VR hybrids; *l* and m = seedlings) · Only those seedlings that were rated "1" in the original test are shown here

Eltern, VR-Kreuzungen und Sämlinge sowie ihr Resistenzgrad (e-, F-, P- und T-Serie = Eltern; 0-Serie = VR-Kreuzungen; *l* und m = Sämlinge) · Nur solche Sämlinge, die bei der ersten Bonitierung die Note 1 erhielten, sind aufgeführt

Derivation	Plant	Original rating	Retested rating
VR backcross to *V. vinifera*	e1—78	2	—
	e1—93	1	1
	e1—100	2	—
	e1—106	3	—
	e2—40	2	—
	e2—82	2	—
	e2—106	1	3
	e4—72	3	—
	e4—76	1	2
	e4—93	4	—
	e4—106	3	—
	e5—124	4	—
	e5—133	4	—
	e5—137	4	—
	e6—32	2	—
V. vinifera hybrids	31—30F	3	—
	31—76F	2	—
	31—123F	2	—
	34—2F	3	—
	37—55F	3	—
	38—105F	3	—
	40—139F	2	—
	41—33F	2	—
	42—1F	1	1
	P76—36	3	—
	T8—43	4	—
VR F_1	037—30	1	1
	041—5	2	—
	041—13	1	1
	041—37	1	1
	041—46	2	—
	042—17	2	—
	042—58	2	—
	043—15	1	1
	043—16	1	1
	043—25	1	1
	043—43	1	1
	043—52	1	1

Parentage	Seedlings	Retested rating
e1—78 × e1—106	*l*1—61	2
	*l*1—71	1
e1—78 × e5—133	*l*1—161	2
e1—78 × e6—32	*l*1—177	3
	*l*2—7	1
e1—93 × e2—40	*l*2—30	3
e2—82 × e1—100	*l*2—53	2
	*l*2—64	1
	*l*2—66	2
	*l*2—78	2
e2—82 × e2—40	*l*2—120	2
e2—82 × e5—124	*l*2—144	1
e2—106 × e2—40	*l*3—55	1
	*l*3—63	2
	*l*3—69	2
e2—106 × e5—133	*l*3—80	2
e2—106 × e6—32	*l*3—109	3
e4—76 × 40—139F	*l*3—130	2
e4—93 × 37—55F	*l*3—134	2
e4—93 × 41—33F	*l*4—12	2
e4—106 × 42—1F	*l*4—147	2
e5—137 × e2—40	*l*5—99	2
e5—137 × e5—13	*l*5—144	1
e5—137 × e6—32	*l*5—169	3
	*l*5—170	2
	*l*5—173	2
	*l*6—11	2
e4—72 × 34—2F	m4—20	2
e4—72 × 38—105F	m4—52	2
	m4—75	2
e4—72 × 40—139F	m4—90	2
	m4—95	2
	m4—101	2
e4—76 × 41—33F	m4—109	1
	m5—2	2
e4—93 × 31—76F	m5—26	2
	m5—38	2
	m5—58	2
e5—124 × T8—43	m5—93	2

Table 2

Ratings of classified parents and distribution of offspring in each class

Bonitierung der klassifizierten Eltern und Verteilung ihrer Nachkommen auf die einzelnen Resistenzklassen

Parents' class[1])	Ratings	Number of offspring in each midparent class	Number of offspring rated as 1	2	3	4
1.5	1, 2	5		2	1	2
2.0	1, 3 or 2, 2	55	5	18	25	7
2.5	2, 3 or 1, 4	312	11	120	136	45
3.0	2, 4 or 3, 3	279	7	69	104	99
3.5	3, 4	133	3	28	39	63
4.0	4, 4	23	1	2	8	12

[1]) Parents were classified according to mean of their ratings, i.e. class "2.0" includes all parents which were rated as "1" and "3" or "2" and "2".

The resistance/susceptibility ratings had standard deviations of 0.474 and 0.847 for parents and offspring, respectively, indicating that the parents have been selected for resistance to the nematode. This fact is also verified by the average ratings of parents and offspring. The average ratings for parents and offspring were 2.600 and 2.916, respectively.

The heritability of resistance to the nematode on the basis of offspring-midparent regression is 0.391 ± 0.06. Fig. 3 shows the relationship between parental and offspring performance, where the midparent performance has been repeated within progenies (4). Thus, our results indicate that 39 % of the variation is due to the additive effects of genes and the remainder would be due to non-additive genetic effects and environment.

Breeding stocks with high heritability can be improved by simple and relatively inexpensive "mass selection" methods. Progeny tests are not necessary since potential parents can be identified from inferior parents in segregating populations by direct measurements of performance. With high heritability, the breeder is also free to allow selected parents to mate randomly, *inter se,* and need not resort to the expensive techniques of positive and negative assortative matings that are required when overdominance and epistasis have important effects on performance (7).

Estimates of heritability obtained in several perennial clonal horticultural species such as sweet cherry (11), walnut (12), strawberry (13), peach (14), plum and prune (15), almond (17), and grapes (8 and 21) have been found to be very useful guides in a cultivar breeding program to ensure relatively rapid improvement of breeding stocks by direct mass selection methods.

The population analyzed in this study contains considerable additive genetic variability for the trait studied. The precision of the heritability estimate is also high. Thus, the heritability should provide a reliable predictor of genetic gain for several generations when parents are selected on the basis of their own performances and their subsequent mating *inter se.* More complex breeding procedures (such as those which employ progeny testing and inbreeding that are designed to exploit non-additive genetic effects) appear to be unnecessary in these vines.

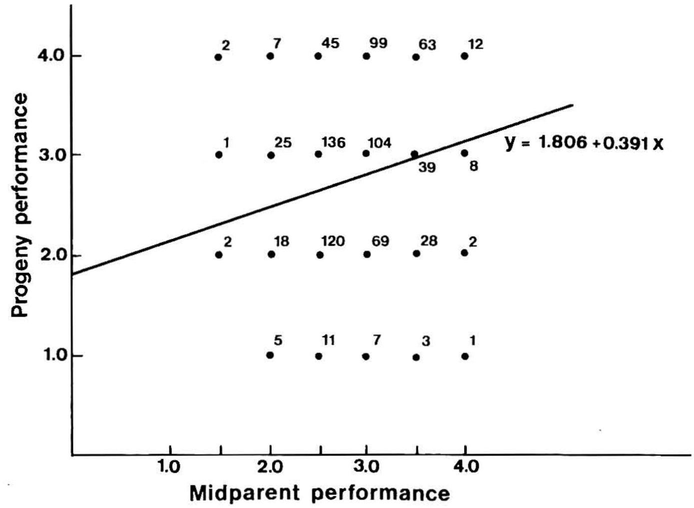

Fig. 3: Heritability of nematode resistance. "1" indicates the most resistant and "4" the most susceptible. Numbers by the points are the number of progenies showing that rating (see also Table 1).

Heritabilität der Nematodenresistenz. Klasse 1 = höchste Resistenz, 4 = größte Anfälligkeit. Zahlen neben den Punkten = Anzahl der Nachkommen mit der jeweiligen Bonitierungsnote (vgl. auch Tabelle 1).

The expected genetic gain per generation, Δg, can be predicted from the equation $\Delta g = i\delta_p h^2$, where δ_p is the standard deviation of parental population, h^2 is heritability and i is the intensity of selection (difference between the mean of selected parents and the mean of the population from which the parents were selected), expressed in standard deviations from the population mean (7). Assuming 5 % of the offspring population is selected ($i = 2.06$), the genetic gain in the next generation would be 0.68, indicating that selection of resistant seedlings as parents should be very effective in improving the mean of resistance of this foundation stock. A gain of approximately 24 % of the mean of the parental population should be possible each generation.

These results would be much more useful in cases when vine breeders have to breed, at the same time, for other quantitative fruit characters such as crop weight, berry size, cluster size, etc. In cases where several quantitative characters are to be improved simultaneously, correlations among the traits and their heritability are estimated (11). Where the correlations are large, selection efficiency should be improved on the basis of selection indices (1 and 6).

The retested plants (rated as "1" or "2"), since their resistance to the nematode has been verified, could be used as resistant rootstocks. The same plants were tested for grape phylloxera resistance (10). Some of these are also resistant to phylloxera and could be used either as rootstocks for areas where both pests are destructive, or used in other vine improvement projects to combine resistance with desirable fruit characters. The seedlings and parents have also been tested for desirable fruit characters such as crop weight, cluster weight, berry size, etc., and their heritabilities determined. If we find some vines with desirable table grape characters and also resistant to either nematodes, phylloxera or both, they could be propagated and released as new varieties. On the other hand, if some vines possess some of the desirable characters, but not others, they could be combined with the others in order to improve their deficiencies and then be released as a new cultivar, especially for home garden use in problem areas.

Summary

A population of 807 offspring of 46 families, generated by crosses among 26 parents (some quasi-F_1 hybrids of *V. vinifera* × *V. rotundifolia*), the parents, 12 *V. vinifera* × *V. rotundifolia* (VR) hybrids, Muscat of Alexandria and Dog Ridge (controls) were all grown in the vineyard of the University of California at Davis and were tested in a greenhouse for resistance to the sedentary endoparasite root-knot nematode (*Meloidogyne incognita acrita* CHIT.). Some of the seedlings and parents and almost all the VR hybrids showed resistance to the nematode and ratings were verified by retesting.

The heritability was estimated to be 0.391 ± 0.06. The expected average gain of the progeny of randomly mated parents ranked in the upper 5 % of the parental generation were calculated. The result indicates that relatively rapid genetic gain is to be expected in the population based on their own performance and subsequent mating, *inter se,* without use of the more expensive methods of progeny testing and inbreeding which are used to exploit non-additive portions of the genetic variability.

The uses of the resistant plants as rootstocks and the longer term combination with desirable economic characters are discussed.

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