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# Further evidence of phylloxera biotypes: Variations in the tolerance of mature grapevine roots related to the geographical origin of the insect

by

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## Weitere Hinweise auf Reblausbiotypen: Unterschiedliche Toleranz der verholzten Rebwurzel in Beziehung zur geographischen Herkunft des Insekts

Zusammenfassung: In standardisierten Gewächshausversuchen wurden an einem neuseeländischen und einem deutschen Standort fünf Unterlagen (*Vitis*-Artkreuzungen) und eine *V.-vinifera*-Sorte mit Rebläusen (*Dactylosphaera vitifolii* SHIMER) der jeweiligen Region infiziert. Am Ende des 2. Versuchsjahres wurde die Anzahl der an den verholzten Wurzeln gebildeten Tuberositäten ermittelt sowie anhand mikroskopischer Schnitte ihre Reblaustoleranz bonitiert. Als Toleranzmerkmal diente die Abriegelung der Reblausnekrosen durch Wundperiderm.

In beiden Ländern wiesen die Wurzeln der Sorten ARG 1 und Müller-Thurgau die höchste Tuberositätenhäufigkeit auf. Die wenigsten Tuberositäten fanden sich an der Unterlage 3309 C bei Infektion mit neuseeländischen Rebläusen. Geographisch bedingte Unterschiede der durchschnittlichen Reblaustoleranz, die nicht sehr hoch, aber statistisch signifikant waren, wurden für 420 A, SO 4, 1202 C und Müller-Thurgau nachgewiesen.

Die Reblaustoleranz der Sorten 420 A, SO 4 und 1202 C war ausreichend bis gut, 3309 C lag im mittleren Toleranzbereich, ARG 1 und Müller-Thurgau wurden als ungenügend tolerant benotet. Bei Befall von ARG 1 durch neuseeländische Rebläuse griffen die Nekrosen jedoch nicht auf die Leitungsbahnen der Wurzel über — selbst dann nicht, wenn das Wundperiderm unterbrochen war oder fehlte. Diese Unterlage wird daher — entgegen der erteilten Bonitierungsnote — als unter neuseeländischen Bedingungen ausreichend tolerant eingestuft. 3309 C wird aufgrund der sehr niedrigen Tuberositätenhäufigkeit ebenfalls als praktisch tolerant gegenüber neuseeländischen Rebläusen angesehen.

Die zwischen den beiden Versuchsorten beobachteten Unterschiede der Tuberositätenbildung liefern ein weiteres Indiz für das Vorkommen unterschiedlicher Reblausbiotypen in Neuseeland und Deutschland.

Key words: phylloxera, biotype, rootstock, wine grape variety, tuberosity, gall, tolerance, New Zealand, Germany.

## Introduction

In a previous paper evidence was shown that strain or biotype differences existed between a New Zealand and a German phylloxera population (KING and RILLING 1985). While the study tested the resistance of leaves and rootlets to galling, the present investigation focussed on the tolerance of the woody roots to attack by these two phylloxera populations.

The decisive role of tuberosities for survival of phylloxera-infested grapevines, known since the early work of MILLARDET (1898) and RAVAZ (1897), is generally recognized. Early differentiation of a continuous wound periderm is essential to prevent penetration of decay to the vascular system of the woody roots (RAVAZ 1897; PETRI 1909; ABASSADZE *et al.* 1930; MANZONI 1950; PARNIEWSKI 1963; BOUBALS 1966; KISKIN 1966; SOKOLOVSKAYA 1966; ZOTOV *et al.* 1966; for a general review see also GALET 1982).

During the last few years the list of papers describing the occurrence of phylloxera biotypes in different parts of the world has been continued. In California, GRANETT *et al.* (1985, 1987 a, 1987 b) observed different resistance on the roots of certain grapevine genotypes to two phylloxera strains living in close proximity. In Ohio, WILLIAMS and SHAMBOUGH (1988) described two sympatric biotypes differing in induction of leaf galls on a number of grapevine hosts; the authors also reported serological peculiarities of the biotypes. In France, SONG and GRANETT (1990) found different resistance of woody grapevine roots dependent of the origin of phylloxera, suggesting host-based rather than geographically based races. (For other literature see GALET 1982; KING and RILLING 1985.) Genetic changes in phylloxera, resulting in improved adaptation to hosts, are also suggested by the observations of Italian and other authors quoted by CROVETTI and ROSSI (1989), who reported increased formation of phylloxera galls on leaves of *Vitis vinifera.*

Variation in aggressiveness of phylloxera has important consequences for the stability of host plant tolerance (and resistance) and must be considered in the introduction of rootstocks into new grapegrowing regions. The aim of this study is to clarify the situation between New Zealand and Germany with regard to tolerance of the woody roots, which is essentially determined by tuberosity formation.

For clarity, the definitions of the terms 'resistance' and 'tolerance' as used in this paper and adopted from DE PONTI (1977, p. 637) are added: '... two basically different mechanisms of a plant to withstand a parasitic attack can be distinguished: resistance (vs. susceptibility) and tolerance (vs. sensitivity). ... *Resistance* is the complex of characters of a host that reduces the reproduction of a parasite. *Tolerance* is the ability of a host to endure the occupation by a parasite.'

## Materials and methods

The tests were performed under standardized glasshouse conditions at Ruakura Research Centre from December 1982 to June 1984, and at Experimental Station Langenscheiderhof of the Institute for Grapebreeding Geilweilerhof with cuttings propagated from New Zealand derived wood in July 1984 and then overwintered to synchronize the young plants with the northern hemisphere growing rhythm; the infestation phase with German phylloxera lasted from April 1985 to December 1986. The grapevine material, phylloxera populations and culturing conditions were the same as described earlier for leaf gall and nodosity tests (KING and RILLING 1985).

New Zealand derived grapevines comprised rootstocks 420 A (*V. berlandieri* × *V. riparia*), SO 4 (*V. berlandieri* × *V. riparia*), 3309 C (*V. riparia* × *V. rupestris*), 1202 C (*V. vinifera* × *V. rupestris*), ARG 1 (AXR 1) (*V. vinifera* × *V. rupestris*), and the wine grape variety Müller-Thurgau (*V. vinifera*). The number of test plants evaluated is

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Abb. 1: Querschnitte durch reblausbefallene verholzte Rebwurzeln (Ø 2—4 mm) zur Illustration der verschiedenen Toleranzgrade. Die Pfeile weisen auf Wundperiderm hin. Die abgebildeten Beispiele spiegeln nicht unbedingt die durchschnittliche Befallsreaktion einer Sorte wider. — Bonitierungsnote 1: Müller-Thurgau (G), 2: SO 4 (G), 3: SO 4 (G), 4: 3309 C (NZ), 5: ARG 1 (NZ), 7: 420 A (NZ), 9: SO 4 (NZ). Weitere Erläuterungen siehe unter „Materials and methods".

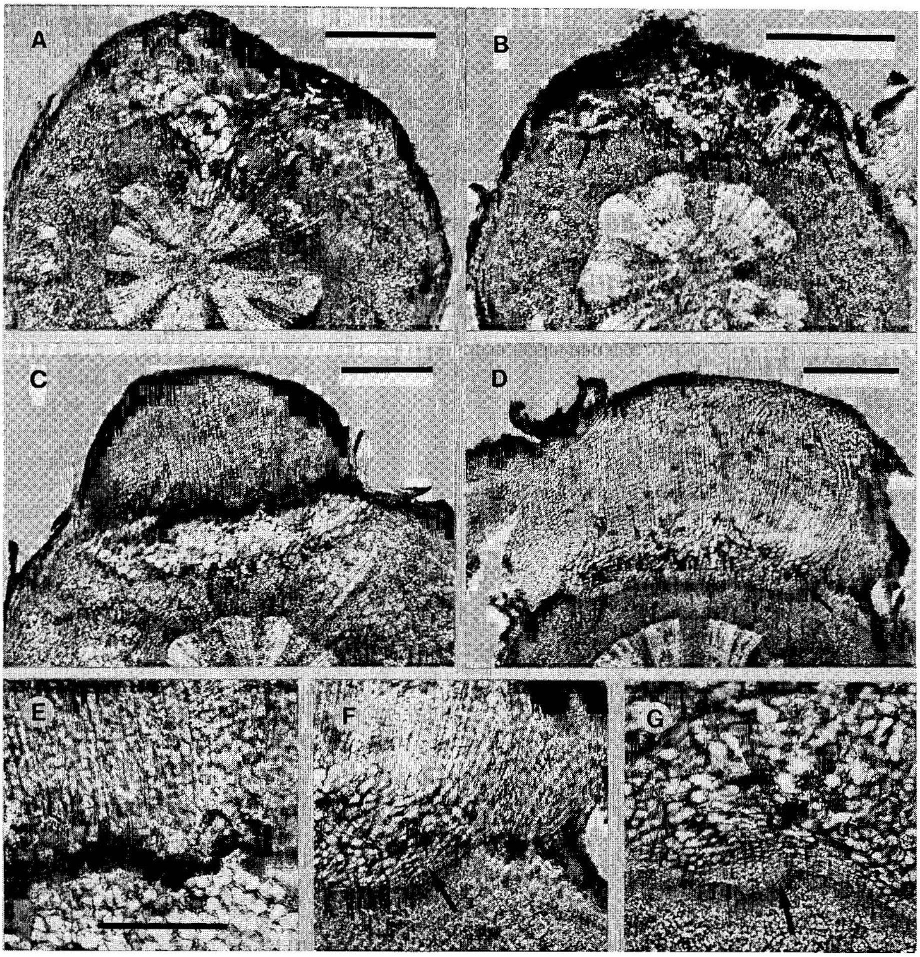


Fig. 3: Woody roots of variety ARG 1 infested by German (G) or New Zealand (NZ) phylloxera. — A)Degree 1, B) degree 3 tuberosity of ARG 1 (G) with necroses penetrating. C) Degree 1, D) degree 3 tuberosity of ARG 1 (NZ) with cushion-like neoformations; no necroses penetrating. E) More enlarged detail from (C) showing layer of darkened parenchymous cells underlying the vertical cell rows. F) Detail from (D) showing cell darkening as in (E) (right) and partial formation of wound periderm as in (G) (left). G) Continuous periderm layer sealing a degree 5 ARG 1 (NZ) tuberosity (compare Fig. 1, Degree 5). Tumor cells above periderm are enlarged and irregularly arranged, as is the case in (F) left part. — Arrows indicate wound periderm. Bars in (A, B, C, D) correspond to 500 µm, bar in (E) is equal to 250 µm.

Verholzte Wurzeln der Sorte ARG 1, von deutschen (G) oder neuseeländischen Rebläusen (NZ) befallen. — A) Mit Note 1, B) mit Note 3 bewertete Tuberosität von ARG 1 (G); Nekrosen nicht abgeriegelt. C) Tuberosität der Note 1, D) der Note 3 von ARG 1 (NZ) mit polsterförmigen Wucherungen; keine fortschreitende Nekrotisierung. E) Ausschnittvergrößerung aus (C) mit einer Schicht dunkelgefärbter Parenchymzellen an der Basis der vertikalen Zellreihen. F) Ausschnitt aus (D) mit dunkelgefärbten Zellen wie in (E) (rechts) und unvollständiger Entwicklung eines Wundperiderms wie in (G) (links). G) Geschlossene Wundperidermschicht, die eine Tuberosität der Note 5 von ARG 1 (NZ) abriegelt (vgl. Fig. 1, Note 5). Die Tumorzellen oberhalb des Periderms sind vergrößert und unregelmäßig angeordnet; dasselbe gilt für (F) links. — Die Pfeile weisen auf Wundperiderm hin. Die Balken in (A, B, C, D) entsprechen 500 µm, der Balken in (E) entspricht 250 µm.

shown in Tables 2 and 3.

Phylloxera populations included root gall forms from New Zealand (NZ) and leaf gall forms from the German station (G). As shown by KING and RILLING (1985), there was no difference in the response of grapevine roots to either radicicole or gallicole phylloxera. '(NZ)' or '(G)' following the variety names indicate the origin of phylloxera and the experimental site, respectively.

In both trials, about 10 vines to be used as controls for growth measurements were kept under the same environmental conditions in uninfested glasshouses. Weights of annual shoots and of root mass were recorded after the 2nd growth period.

Infested pieces of woody roots from the two stations were preserved in alcohol and, for uniformity of screening, examined at one place (Geilweilerhof). The frequency of tuberosities was generally determined as the number of symptoms/100 cm of root length. In the New Zealand material of varieties 420 A, SO 4 and 1202 C it was, however, not possible to distinguish single tuberosities; in these cases the extension of the discoloured and deformed root zones is given as % of the total root length.

Root pieces with symptoms of phylloxera infestation, taken randomly, were transversally sectioned by use of a hand microtome. 40 μm sections collected in water were observed by means of a dissecting microscope or, enclosed in glycerol, by a light microscope. Application of lipoid dyes for staining cork incrustations of protective tissue was not helpful, as the wound periderm is clearly identified by its histological aspect (Fig. 3, G).

The degree of tolerance to phylloxera attack was judged according to O.I.V. code no. 462 (O.I.V. 1983), which uses a scale of 1, 3, 5, 7 and 9 points. Two intermediate classes, given 2 and 4 points, respectively, were inserted, as the five O.I.V. classes did not cover all the phylloxera symptoms observed. The single classes are defined as follows (Fig. 1; for better understanding compare Fig. 2):

Degree 1: No wound periderm is formed, necrosis penetrates the vascular system.

Degree 2: A continuous layer of wound periderm is formed, but necrosis spreads behind the inner side of this layer over the vascular system.

Degree 3: Wound periderm is discontinuous and necrosis penetrates the vascular system through the gap.

Degree 4: Wound periderm is nearly closed except for a narrow gap between adjacent phloem cupolae. Necrosis penetrates along a ray of the 1st order into the xylem, where it is often stopped at the border between 2nd and 1st year secondary xylem.

Degree 5: A continuous layer of wound periderm is formed; necrosis is completely isolated but extends to peripheral parts of the vascular system.

Degree 7: Necrosis is completely isolated outside the vascular system by a continuous layer of wound periderm.

Degree 9: Puncture-shaped necrosis, isolated superficially in the bark. No swelling of the root. Interpreted as a hypersensitivity reaction. Phylloxera development incomplete.

Assessments of degree 5 or higher indicate tolerance; below 5 sensitivity to phylloxera damage.

Degree 1, 2 and 3 tuberosities where there is a lack or insufficient formation of cork layers and destruction of vascular tissues correspond to the root behaviour defined by BOUBALS (1966) as resistance class 3. It must be noted, however, that BOUBALS' classes also include the size and frequency of tuberosities. Degrees 4 and 5 correspond to the histological description of class 2 by BOUBALS. Our degrees 7 and 9 are identical with BOUBALS' classes 1 and 0, respectively.

Data was statistically analysed by T-tests where appropriate.

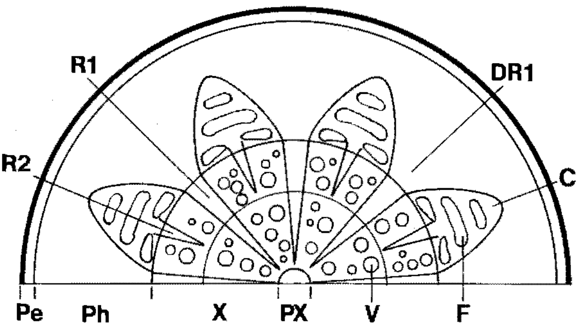


Fig. 2: Schematic view of transversally sectioned 2-year-old grapevine root, showing the main anatomical structures. — C = phloem cupola, DR1 = dilation of ray R1, F = plate of phloem fibers ('Hartbast'), Pe = periderm with outer cork layer and rhytidomes, Ph = secondary phloem, PX = primary xylem, R1 = secondary ray of 1st order which crosses the secondary xylem, R2 61 secondary ray of the 2nd order which terminates inside the phloem cupola, V = large vessel, X = secondary xylem. The complex of phloem cupolae together with the xylem is referred to as 'vascular system'.

Schematisierte Darstellung einer quergeschnittenen 2jährigen Rebwurzel mit den wichtigsten anatomischen Strukturen. — C = Phloemkuppel, DR1 = Verbreiterung des Markstrahls R1, F = Hartbastplatte, Pe = Periderm mit äußerer Korkschicht und abgestoßenen Zellagen, Ph = sekundäres Phloem, PX = primäres Xylem, R1 = sekundärer Markstrahl 1. Ordnung, der das sekundäre Xylem durchzieht, R2 = sekundärer Markstrahl 2. Ordnung, der in der Phloemkuppel endet, V = weite Trachee, X = sekundäres Xylem.

## Results

### Effects of phylloxera on vegetative growth

When comparing the vegetative yields between the two countries (Table 1), one should consider that the New Zealand phylloxera population did not cause leaf galling. There were also regional differences in formation of nodosities (King and Rilling 1985). Thus, the results must be treated with caution. In most cases the effects of tuberosities on vegetative growth cannot be separated, though generally grapevines will be most severely stressed by the loss of woody roots.

Comparison of the weight of annual shoots produced by the uninfested control plants during the 2nd growing period showed a trend to higher shoot weights under German conditions. With New Zealand controls, the root weights were often higher. Among infested plants, in Germany shoot and root growth was generally reduced compared with controls. In infested New Zealand grapevines, production of both shoots and roots was more often similar to that of their controls or even higher.

The specific varietal response to phylloxera attack is quantified by the per cent changes of infested vines. In both countries Müller-Thurgau showed the heaviest depression of vegetative productivity. Highest shoot weights, unexpectedly higher than controls, were observed at both sites with ARG 1, whereas root growth of 1202 C was greatest in both countries.

### Effects of phylloxera on woody roots

#### Frequency of tuberosities

Table 2 shows the frequency of tuberosities induced by the two phylloxera populations. Contrasting to the German trial, in the majority of varieties exposed to the New

Table 1

Average shoot weight (2nd-year growth) and root weight of five rootstocks and *V. vinifera* cv. Müller-Thurgau, non-infested and infested by a New Zealand and a German phylloxera population

Durchschnittliches Sproßgewicht (im 2. Befallsjahr gebildete Sproßmasse) und Wurzelgewicht von fünf Unterlagssorten und der *V.-vinifera*-Sorte Müller-Thurgau, ohne Reblaus und bei Befall mit einer neuseeländischen und einer deutschen Reblauspopulation

| Variety | Shoots (g dry wt/vine) | | | | Roots (g fresh wt/vine) | | | |
|---|---|---|---|---|---|---|---|---|
| | New Zealand | | Germany | | New Zealand | | Germany | |
| | Control | Infested | Control | Infested | Control | Infested | Control | Infested |
| 420 A | 9.8 | 7.7 (89) | 11.7 | 10.7 (91) | 51.8 | 42.4 (82) | 51.5 | 42.4 (82) |
| SO 4 | 8.5 | 8.6 (101) | 11.7 | 8.5 (73) | 85.5 | 90.3 (106) | 56.0 | 44.6 (80) |
| 3309 C | 7.4 | 7.4 (100) | 9.2 | 7.9 (86) | 80.4 | 64.4 (80) | 51.5 | 27.4 (53) |
| 1202 C | 11.6 | 12.0 (103) | 14.8 | 13.0 (88) | 60.9 | 81.9 (134) | 44.5 | 40.8 (92) |
| ARG 1 | 9.0 | 9.5 (106) | 11.8 | 14.1 (120) | 81.6 | 95.2 (117) | 49.8 | 32.2 (65) |
| Müller-Thurgau | 8.2 | 3.8 (46) | 11.9 | 7.8 (66) | 79.2 | 29.8 (38) | 82.5 | 35.4 (43) |

Figures in parentheses in colums 'Infested' are percentages related to the corresponding control values (= 100 %).

Zealand phylloxera, contiguous darkening of the affected root portions prevented the distinction of single tuberosities. Comparison between the countries is limited to two varieties. ARG 1 (G) and Müller-Thurgau (G) were significantly less infested than their New Zealand counterparts. Frequency of tuberosities caused by the German phyllox-

Table 2

Average frequency of tuberosities formed on woody roots of five rootstocks and *V. vinifera* cv. Müller-Thurgau infested by a New Zealand and a German phylloxera population

Durchschnittliche Häufigkeit der Tuberositäten an den verholzten Wurzeln von fünf Unterlagssorten und der *V.-vinifera*-Sorte Müller-Thurgau bei Befall mit einer neuseeländischen und einer deutschen Reblauspopulation

| Variety | New Zealand phylloxera | | | German phylloxera | | | LSD for frequency |
|---|---|---|---|---|---|---|---|
| | Number of vines | Total root length (cm) | Av. frequency of tuberosities | Number of vines | Total root length (cm) | Av. frequency of tuberosities²) | |
| 420 A | 19 | 770 | 72 ± 34¹) | 8 | 463 | 16 ± 9 | — |
| SO 4 | 16 | 703 | 31 ± 18¹) | 12 | 1 008 | 19 ± 12 | — |
| 3309 C | 21 | 1 128 | 2 ± 8¹) | 14 | 1 050 | 15 ± 13 | — |
| 1202 C | 13 | 624 | 52 ± 32¹) | 16 | 1 005 | 37 ± 43 | — |
| ARG 1 | 19 | 883 | 487 ± 253²) | 12 | 838 | 161 ± 134 | 254.4*** |
| Müller-Thurgau | 20 | 674 | 355 ± 106²) | 12 | 885 | 82 ± 41 | 97.1*** |

¹) Dark coloured root portion as % of total root length.
²) Number of tuberosities/100 cm of root length.
*** Significant difference at P = 0.001.

Table 3

Average tolerance shown by woody roots of five rootstocks and *V. vinifera* cv. Müller-Thurgau infested by a New Zealand and a German phylloxera population

Durchschnittliche Toleranz der verholzten Wurzeln von fünf Unterlagssorten und der *V.-vinifera*-Sorte Müller-Thurgau bei Befall mit einer neuseeländischen und einer deutschen Reblauspopulation

| Variety | New Zealand phylloxera | | | | German phylloxera | | | | LSD for tolerance |
|---|---|---|---|---|---|---|---|---|---|
| | Number of vines | Number of tube-rosities | Av. degree of tolerance | Range | Number of vines | Number of tube-rosities | Av. degree of tolerance | Range | |
| 420 A | 17 | 67 | 7.0 ± 0.4 | 7 | 8 | 34 | 6.4 ± 1.3 | 3—7 | 0.46* |
| SO 4 | 15 | 51 | 6.8 ± 0.7 | 4—7 | 12 | 55 | 6.2 ± 1.5 | 2—7 | 0.46* |
| 3309 C | 6 | 14 | 4.9 ± 1.4 | 4—7 | 14 | 70 | 5.1 ± 1.7 | 2—9 | 0.86 NS |
| 1202 C | 13 | 49 | 7.0 ± 0 | 7 | 15 | 67 | 6.2 ± 1.6 | 1—9 | 0.68*** |
| ARG 1 | 18 | 72 | 4.1 ± 2.3 | 1—7 | 12 | 84 | 4.9 ± 2.3 | 1—7 | 0.73 NS |
| Müller-Thurgau | 21 | 84 | 3.5 ± 1.6 | 1—7 | 12 | 60 | 4.2 ± 2.1 | 1—7 | 0.65* |

*, *** = Significant differences at P = 0.05 or P = 0.001, NS = no significant difference.

era increased in the order 3309 C, 420 A, SO 4, 1202 C, Müller-Thurgau, ARG 1. In the New Zealand experiment, 3309 C clearly had the lowest infestation, but due to differences in the recording of tuberosity frequency, an overall comparison among varieties would be speculative.

## Classes of tuberosities

Within a given variety at an experimental site, generally several levels of tolerance were evident (Table 3, Figs. 1 and 3). Exceptions were 420 A (NZ) and 1202 C (NZ), where only degree 7 was registered.

Though the average values of identical varieties did not differ greatly between countries, significant differences were calculated for varieties 420 A, SO 4, 1202 C and Müller-Thurgau, when infested with either New Zealand or German phylloxera. No significant differences were found with 3309 C and ARG 1.

In both countries, rootstock varieties 420 A, SO 4 and 1202 C exhibited sufficient to good isolation of necrotic tissues. 3309 C and ARG 1 ranged around the threshold of tolerance. Müller-Thurgau was, as expected, sensitive to root rot.

Remarkable histological differences were observed between ARG 1 (G) and ARG 1 (NZ) tuberosities of degrees 1 or 3. The galls induced by German phylloxera showed the typical aspect of these classes — irregular and hypertrophic cell growth together with progressive necrosis, due to missing or discontinuous protective layers (Fig. 3, A, B). The prominent tuberosities of ARG 1 (NZ) were light-brown in colour as in the normal root. Transverse sections revealed peripheral thick cushion-like neoformations with a very regular cell arrangement (Fig. 3, C, D). This resulted obviously from a continuous series of undisturbed periclinal cell divisions, forming strands of isodiametric cells. Centripetally, a layer of darkened parenchymous cells was visible, indicating biochemical alterations of the cell contents. Despite lack of cork layers, root rot was not penetrating.

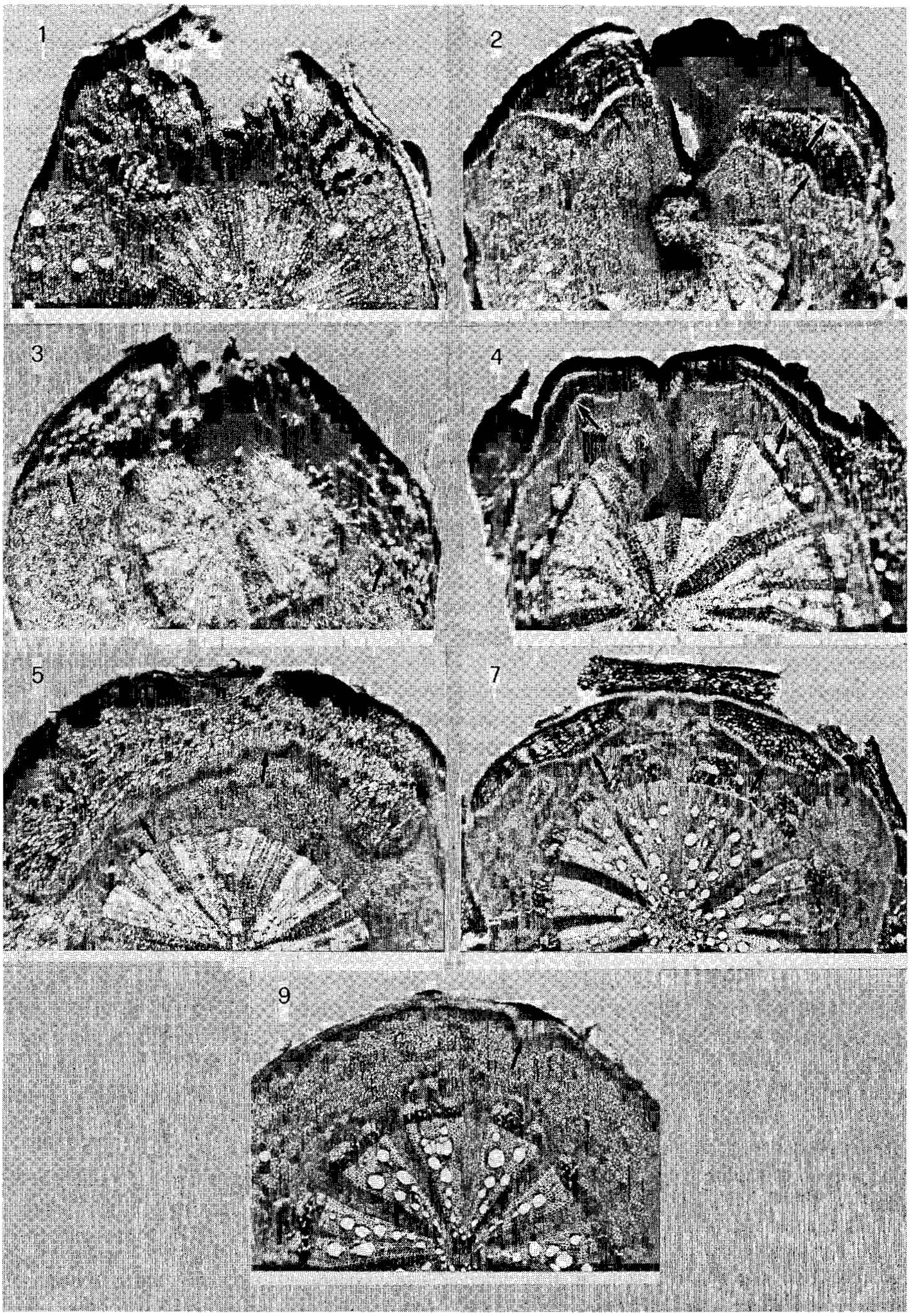


Fig. 1: Cross sections through infested mature grapevine roots illustrating the degrees of tolerance to phylloxera (root ∅ 2—4 mm). Arrows indicate wound periderm. The examples shown do not necessarily reflect the average ratings of varieties. — Degrees 1: Müller-Thurgau (G), 2: SO 4 (G), 3: SO 4 (G), 4: 3309 C (NZ), 5: ARG 1 (NZ), 7: 420 A (NZ), 9: SO 4 (NZ). For further explanation compare 'Materials and methods'.

## Discussion

Differences in the tolerance of identical grapevine varieties to New Zealand or German phylloxera, though not exceeding 1 point, were significant in 4 out of 6 cases. In the New Zealand trial, there was a tendency to more uniformity within varieties. In the varieties 420 A (NZ) and 1202 C (NZ) all tuberosities examined belonged to the same level of high tolerance (degree 7). In the German trial, the intravarietal variation of phylloxera response was increased.

As seen from the average ratings, in both countries tolerance of the woody roots to phylloxera attack was medium to high in the rootstock varieties 420 A, SO 4 and 1202 C. The rating of 3309 C near the tolerance/sensitivity limit (around degree 5) was unexpected. In the New Zealand trial, however, the doubtful isolation response of this rootstock was counteracted by the sparse occurrence of tuberosities. This is in agreement with its practical tolerance.

Following the definitions of tuberosity classes, ARG 1 was ranked sensitive to both New Zealand and German phylloxera (degrees 4.2 and 4.9, LSD non-significant). In ARG 1 (NZ) necroses did not penetrate, even if cork formation was unsatisfactory. These roots must be judged as having sufficient tolerance in contrast to sensitivity under German conditions. It is unclear if the thick, regularly structured tumor tissue observed in the case of New Zealand phylloxera acts like a wound periderm, or if an unidentified biochemical barrier prevents penetrating of necrotic agents.

When comparing the present screening results with Boubals' (1966) data, there was approximate coincidence with SO 4 (NZ/G), ARG 1 (G) and Müller-Thurgau (NZ/G). 420 A (NZ/G) and 3309 C (NZ/G) were rated inferior, and 1202 C (NZ/G) was superior to the rating established by Boubals. Because of their inconsistent phylloxera response, *V. vinifera* × *V. rupestris* hybrids 1202 C and ARG 1 are not permitted in German viticulture. According to Galet (1988) they may do well on profound, sandy, cool or irrigated soils. While failing in dry, hot regions such as the Mediterranean, they

Table 4

Comparison of responses of five rootstocks and *V. vinifera* cv. Müller-Thurgau to infestation by a New Zealand and a German phylloxera population

Vergleich der Reaktionen von fünf Unterlagssorten und der *V.-vinifera*-Sorte Müller-Thurgau auf Befall mit einer neuseeländischen und einer deutschen Reblauspopulation

| Variety | New Zealand phylloxera | | | German phylloxera | | |
|---|---|---|---|---|---|---|
| | Leaf galls[1]) | Nodosities[1]) | Tuberosities[2]) | Leaf galls[1]) | Nodosities[1]) | Tuberosities[2]) |
| 420 A | – | + | – | – | – | – |
| SO 4 | – | – | – | + | + | – |
| 3309 C | – | – | ± | + | + | – |
| 1202 C | – | –(+) | – | – | + | – |
| ARG 1 | – | –(+) | –[3]) | + | – | ± |
| Müller-Thurgau | – | + | + | + | + | + |

[1]) + = Leaf galls or nodosities formed, – = no leaf galls or nodosities formed, –(+) = nodosities rarely formed.
[2]) + = Necrosis penetrated, – = necrosis isolated, ± = intermediate reaction.
[3]) Atypcial isolation reaction.
Data on leaf galls and nodosities from King and Rilling (1985).

may perform satisfactorily in California, Australia and New Zealand (for literature see KING and RILLING 1985). Their high tolerance to New Zealand phylloxera reported earlier (KING *et al.* 1982) is confirmed by the study of tuberosities.

The significantly different responses of certain varieties to New Zealand and German phylloxera indicate deviations in phylloxera biology between the two countries. Though not as obvious as with leaf gall and nodosity formation (KING and RILLING 1985), they support further evidence of different phylloxera strains or biotypes at the two experimental sites.

A schematized comparison of the response of mature roots to phylloxera attack and nodosity formation on rootlets (besides leaf gall formation) is shown in Table 4. As formation of galls is obligatory for development and reproduction of phylloxera, the presence/absence of nodosities and leaf galls is a measure of susceptibility/resistance to the insect. Penetration/isolation of tuberosity necroses, on the other hand, indicates sensitivity/tolerance of the root system to the pest. As is to be expected from the different nature of resistance and tolerance, it is seen that tolerance of mature roots does not have to be correlated with resistance of the rootlets, and vice-versa (e.g. SO 4 (G), 420 A (NZ)). High resistance and high tolerance may occur together (SO 4 (NZ)), and low resistance may be combined with low tolerance (Müller-Thurgau (NZ/G)). It has also been shown that nodosity formation due to German phylloxera need not be parallel to leaf gall formation.

The results demonstrate that the test for tolerance of the mature grapevine root, which is the decisive character for survival of the plant, cannot be replaced by observations of phylloxera development on the rootlets alone. Furthermore, it is important to use for inoculation tests the phylloxera population of the region where planting of a certain rootstock is planned.

## Summary

Five rootstocks (*Vitis* spp. hybrids) and a *V. vinifera* cultivar were phylloxera infested in standardized glasshouse trials in New Zealand and Germany. At the end of the second growing season the formation of tuberosities on the woody roots was evaluated.

In both countries, highest frequency of tuberosities was found on roots of varieties ARG 1 and Müller-Thurgau. Tuberosities were rare on 3309 C infested by New Zealand phylloxera. Differences in the average degree of phylloxera tolerance, based on isolation of necroses by wound periderm, were small between the two countries, but significant in case of 420 A, SO 4, 1202 C and Müller-Thurgau.

Phylloxera tolerance was scored as sufficient to good with varieties 420 A, SO 4 and 1202 C. 3309 C ranged medium, whereas ARG 1 and Müller-Thurgau were rated as sensitive. However, in ARG 1 infested by the New Zealand phylloxera necroses did not penetrate, even when wound periderm was lacking or incomplete. This rootstock is therefore assessed as having sufficient tolerance under New Zealand conditions, thus deviating from the numerical rating. 3309 C is, due to the low frequency of tuberosities, also considered as having practical tolerance to New Zealand phylloxera.

The differences in tuberosity formation observed between the two experimental sites support further evidence of two different phylloxera biotypes between New Zealand and Germany.

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## Literature cited

ABESSADZE, K. J.; MAKAREVSKAJA, E. A.; ZCHAKAJA, K. E.; 1930: Über die verschiedenen Grade der Widerstandsfähigkeit gegen Reblaus allgemein verbreiteter georgischer Rebensorten, bedingt durch die Unterschiede in der anatomischen Struktur ihrer Wurzeln [Russ.]. Scientific Papers of the Applied Sections of the Tiflis Botanical Garden (7).

BOUBALS, D.; 1966: Etude de la distribution et des causes de la résistance au phylloxéra radicicole chez les Vitacées. Ann. Amélior. Plantes **16**, 145—184.

CROVETTI, A.; ROSSI, E.; 1989: Field and laboratory observations on some eco-ethological aspects of the grape phylloxera (*Viteus vitifolii* (FITCH)). In: CAVALLORO, E. (Ed.): Influence of Environmental Factors on the Control of Grape Pests, Diseases and Weeds. Proc. Meeting Experts' Group, Thessaloniki, 6—8 October 1987; 107—114. A. A. Balkema, Rotterdam.

GALET, P.; 1982: Les Maladies et les Parasites de la Vigne. Tome II. Les Parasites Animaux. Imprimerie du «Paysan du Midi», Montpellier.

— —; 1988: Cépages et Vignobles de France. Tome 1. Les Vignes Américaines. 2e Ed. Imprimerie Charles Dehan, Montpellier.

GRANETT, J.; GOHEEN, A. C.; LIDER, L. A.; 1987 a: Grape phylloxera in California. Calif. Agriculture **41** (1—2), 10—12.

— —; — —; — —; WHITE, J. J.; 1987 b: Evaluation of grape rootstocks for resistance to Type A and Type B grape phylloxera. Amer. J. Enol. Viticult. **38**, 293—300.

— —; TIMPER, P.; LIDER, L. A.; 1985: Grape phylloxera (*Daktulosphaira vitifoliae*) (Homoptera: Phylloxeridae) biotypes in California. J. Econ. Entomol. **78**, 1463—1467.

KING, P. D.; MEEKINGS, J. S.; SMITH, S. M.; 1982: Studies of the resistance of grapes (*Vitis* spp.) to phylloxera (*Daktulosphaira vitifoliae*). N. Z. J. Exp. Agricult. **10**, 337—344.

— —; RILLING, G.; 1985: Variations in the galling reactions of grapevines: Evidence of different phylloxera biotypes and clonal reaction to phylloxera. Vitis **24**, 32—42.

KISKIN, P. KH.; 1966: Suberin as a factor attributing resistance of grape to phylloxera [Russ.]. Biokhim. Osn. Zashch. Rast., Akad. Nauk SSSR, Inst. Biokhim. 1966, 152—157. [Abst.: Plant Breeding Abst. **39**, 7609].

MANZONI, L.; 1950: Sulle cause della resistenza della viti alla fillossera. Riv. Viticolt. Enol. Conegliano **3**, 47—53.

MILLARDET, A.; 1898: Altérations phylloxériques sur les racines. Rev. Viticult. **10**, 692—698, 717—722, 753—758.

O.I.V.; 1983: Codes des caractères descriptifs des variétés et espèces de *Vitis*. Office International de la Vigne et du Vin, Paris.

PARNIEWSKI, D.; 1963: Untersuchungen über den Wurzelbau und die Reblausresistenz von Unterlagsreben. Weinberg Keller **10**, 537—567.

PETRI, L.; 1909: Über die Wurzelfäule phylloxerierter Weinstöcke. Z. Pflanzenkrankheiten **19**, 18—48.

PONTI, O. M. B. DE, 1977: Resistance in *Cucumis sativus* L. to *Tetranychus urticae* KOCH. 1. The role of plant breeding in integrated control. Euphytica **26**, 633—654.

RAVAZ, L.; 1897: Contribution à l'étude de la résistance phylloxérique. Rev. Viticult. **8**, 109—114, 137—142, 193—199.

SOKOLOVSKAYA, T. I.; 1969: Forming of protective cork layer in grape roots affected with phylloxera [Russ.]. Sel'skokhoz. Biol. **4** (6), 881—884.

SONG, G.; GRANETT, J.; 1990: Grape phylloxera (Homoptera: Phylloxeridae) biotypes in France. J. Econ. Entomol. **83**, 489—493.

WILLIAMS, R. N.; SHAMBAUGH, G. T.; 1988: Grape phylloxera (Homoptera: Phylloxeridae) biotypes confirmed by electrophoresis and host susceptibility. Ann. Entomol. Soc. Amer. **81**, 1—5.

ZOTOV, V. V.; SVETLYAKOVA, R. I.; SOKOLOVSKAYA, T. I.; STOROZHUK, E. M.; KUCHER, A. A.; 1966: Physiology of the resistance of grape to phylloxera [Russ.]. Sel'skokhoz. Biol. 1 (3), 410—420.

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