

GRAPE PHYLLOXERA DAMAGE, ECOLOGY, VARIABILITY, AND MANAGEMENT

Jeffrey GRANETT¹, M. Andrew WALKER², Laszlo KOCSIS³

¹Entomology Department, Univ. of California, USA

²Viticulture & Enology Department, Univ. of California, USA

³Department of Horticulture, Georgikon Faculty of Agronomy, University of Veszprém,
Hungary

ABSTRACT

Grape phylloxera (*Daktulosphaira vitifoliae* Fitch) originated on North American native *Vitis* species. Phylloxera's feeding and damage to wild American *Vitis* is distinct from its feeding and damage to *V. vinifera* (L.). Its feeding on leaves of the American *Vitis* is common and stunts cane growth, but feeding on the leaves of *V. vinifera* is rare. Phylloxera feed on roots less than one year old of both *Vitis* types without causing substantive vine damage. However, feeding on *V. vinifera* mature roots >1 year old results in vine death.

Because phylloxera generally do not feed on mature roots of American *Vitis* species, vine damage does not occur allowing these plants (and their hybrid combinations) to be used as phylloxera resistant rootstocks for more than 100 years. Rootstocks that are hybrids between American *Vitis* and *V. vinifera* can exhibit resistance, but some after a period of efficacy, succumb. Such an occurrence was seen in California with the hybrid AXR#1. We developed a laboratory bioassay based on phylloxera demography to explain the selection of phylloxera virulence associated with AXR#1 and other *V. vinifera* containing rootstocks. This bioassay can also be used to ask whether the pure American rootstocks might also eventually select for phylloxera virulence. Such virulence has been seen in bioassays but has not yet resulted in failure of pure American rootstocks in the field.

Damage of *Vitis* by grape phylloxera is caused by fungal pathogens entering feeding wounds and causing root necrosis. This cause of phylloxera-related damage is essential to understand in case aggressive strains of phylloxera begin to cause damage to resistant rootstocks in the field. In this paper we outline some of the management tactics, including development of better rootstocks that would be necessary were the rootstocks to fail.

Key Words: *Daktulosphaira*, management, pathogen, phylloxera, *Vitis*

IZVLEČEK

ŠKODLJIVOST, BIONOMIJA IN VARIABILNOST TRTNE UŠI (*Daktulosphaira vitifoliae* Fitch) TER VARSTVO VINSKE TRTE PRED TEM ŠKODLJIVCEM

Trsi, ki jih napade trtna uš slabo rastejo, dajejo manjši pridelek in nazadnje odmrejo. Poškodbe trtne uši so posledica hranjenja na koreninah in so vidne na celicah, koreninah, sistemsko na celotnih trsih, v rodnosti vinograda in njegovi vitalnosti. Naša opazovanja kažejo, da so na trsih škodljive tudi različno virulentne glive, ki naselijo poškodovane korenine. Tudi šiške, ki se oblikujejo na listih, so poškodba. Spremlja jih manjša rast poganjkov na podlagah, kar predstavlja gospodarski problem v matičnjakih, kjer pridelujejo podlage. Opažamo tudi pojav trtne uši na listih *Vitis vinifera*, kar pa je manj pogosto in zazdaj ne povzroča škode na trsih ali zmanjšanega pridelka.

Razvoj in uspešnost trtne uši je odvisen od tipa tal, kakovosti korenin in temperature v tleh. Razlike so v stopnji odpornosti ali občutljivosti sort, mikrobiotični aktivnosti v tleh in v genotipih trtne uši. Čeprav lahko virulentnost trtne uši demonstriramo v laboratoriju, so rezultati različne virulentnosti v poljskih

¹ Prof. dr., Davis CA 95616, USA

² Prof. dr., prav tam

³ Assoc. Prof., H-8360 Keszthely, Deak F. ut. 16, Hungary

poskusih, ki so vidni kot poškodbe, lahko opazni le na podlagah z nizko odpornostjo. Pri zelo odpornih podlagah so poškodbe lahko omejene na mlade (lasaste) korenine (nodozitete).

Varstvo pred trtno ušjo je lahko preventivno (karantenski ukrepi) ali aktivno, ko se trtna uš prvič pojavi na listih (kemično varstvo). Najboljša rešitev pa je ponovna zasaditev z visoko odpornimi podlagami. Raziskave interakcij med trtno ušjo in fakultativnimi patogeni z razmerami v tleh in fiziologijo vinske trte bodo pomagale zapolniti vrzeli v znanju in se tako izogniti potencialnim dolgoročnim problemom s podlagami.

1 INTRODUCTION

Grape phylloxera (*Daktulosphaira vitifoliae* Fitch) originated in North America where its hosts are a score of native *Vitis* species. The portion of the grapevine that it feeds upon and damages depends upon the species and geographical location. Feeding can not occur unless galls are formed. Galls on leaves occur on most of the wild American species of *Vitis*. As populations of phylloxera and leaf galls increase on these vines, cane growth decreases (Granett & Kocsis 2000). The European grape, *Vitis vinifera* tends not to have leaf galls, although at some locations leaf galling is beginning to be seen. We do not know the extent of damage that leaf-galling of *V. vinifera* can cause. Phylloxera can feed on immature roots of both *V. vinifera* and American grape species; however no systemic vine damage has been quantified based on this feeding. On American grape species galls rarely form on mature roots (i.e. those >1 year old). However, the heavy galling of mature roots of *V. vinifera* can result in root and vine death. Because mature roots of American *Vitis* species are not damaged, these species are immune to vine damage (though they do host low populations of the insects feeding on the roots and sometimes large populations on the leaves).

This lack of susceptibility of mature roots is the basis for rootstock resistance. Rootstocks may be selections of individual American *Vitis* species, i. e. *V. rupestris* (St. George or du Lot; *V. riparia*, Riparia Gloire) or may be hybrids of several American *Vitis* species or hybrids of American *Vitis* with *V. vinifera*.

Rootstocks of American *Vitis* were first used in the latter part of the 19th century, and they continued to be bred and selected well into the 20th. The resistance of these rootstocks has remained durable, in some cases for more than a century. Rootstocks of pure American *Vitis* have not failed to phylloxera infestations. Rootstock hybrids between American *Vitis* and *V. vinifera* have also been used. Durability of the resistance of these rootstocks has not been as predicable. They sometimes fail after decades of vineyard use. In California, the *V. vinifera* x *V. rupestris* hybrid, AXR#1 (also known as Ganzin 1) was first planted in 1905. By the 1940s it was recognized to have a lower level of phylloxera resistance than pure American rootstocks. However, because of superior viticultural characteristics it was recommended for widespread use in the 1960s. It failed due to phylloxera damage beginning in 1980s. An estimated \$1 billion loss occurred due to this failure between 1985 and 1995.

2 MATERIALS AND METHODS

As a result of AXR#1's failure we developed a bioassay with excised roots to determine demographic characteristics of the types of phylloxera associated with a variety of cultivars (Granett *et al.*, 1983, 1985). Our purpose was to determine the cause of the AXR#1 failure and to screen other rootstocks for phylloxera resistance for use in replanting. In the bioassay we looked at survival – one measure of survival is the proportion of the egg population that survives to the adult stage; developmental rate – which can be expressed as generation time, days from the egg to the median egg of the next generation; and reproductive rate – one measure of this is the number of eggs per female per day.

There are a number of ways these variables can be expressed and combined to predict population size or growth.

3 RESULTS AND DISCUSSION

Results with California phylloxera colonies and various root types suggested that the cause of AXR#1's failure was a selection for more virulent strains of phylloxera and that pure American rootstocks would continue to express resistance against these strains (Granett *et al.*, 1985, 1987). Failure of AXR#1 suggests the question: will rootstocks with pure American parentage eventually select for phylloxera virulence as well? We can look for signs of such failure in the field: initial phylloxera damage in rootstock vineyards. Alternatively, we can take phylloxera populations from rootstock situations and test them with the bioassay. Searches of the literature and discussions with viticulturists suggest no instances of field damage of strongly resistant rootstocks due to phylloxera. Even in regions where populations are high because of leaf galling, rootstock roots remain inviolate. On the other hand, bioassay results suggest that phylloxera are changing, showing in some cases virulence that is greater on rootstocks than on *V. vinifera* (Song & Granett 1990; De Benedictis *et al.*, 1996; Kocsis *et al.*, 1998, 1999, 2000, 2002; Toth *et al.*, 2003). Where virulent phylloxera are indicated by the laboratory bioassay, however, field damage has not been seen. The contradiction between lack of field observations of virulence and the not uncommon bioassay indications of virulence is unexplained. If we accept the bioassay information as a prediction of eventual field failure, how can we prepare for it? We must base any preparation on an understanding of the steps in the progression from phylloxera hatching to vine death.

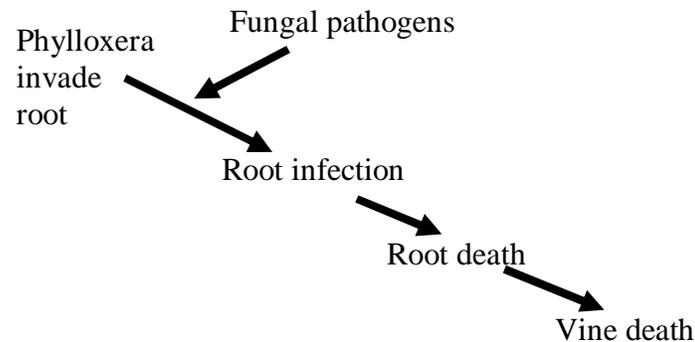


Fig. 1. Steps leading from phylloxera invasion of mature *Vitis* roots to vine death.

This process occurs in several steps (Fig. 1). First, phylloxera must invade mature roots and establish feeding sites to survive and increase their population. They are capable of vectoring soil-borne fungi that are facultative pathogens. Omer *et al.*, (1995) and Granett *et al.*, (1998) have isolated saprophytic as well as pathogenic species from infested roots. An infection can spread radially causing necrosis in the parenchyma and phloem. With time the infection kills the roots and eventually the vine (Omer *et al.*, 1999).

Fossen (2002) surveyed phylloxera infested vineyards of California to collect fungal isolates. Virulence of isolates was established with an excised *V. vinifera* root bioassay determining the proportion of the root circumference that became necrotic in a 5-week period. Some isolates were highly virulent, causing up to 80% necrosis, while other isolates were negligibly virulent.

Isolates showed significantly less virulence on an array of phylloxera resistant rootstocks. Virulence of selected strains was confirmed on potted vines as well as some vines in vineyard environments (unpublished data). This work is continuing but shows that the single weakly-virulent fungal isolate tested by Omer & Granett (2000) was not representative.

Concern about eventual failure of American rootstock resistance to phylloxera demands thought about alternate rootstocks and other control methods. Since little or no phylloxera control has been successfully researched except for use of conventional rootstocks, this is new research territory. What options can we consider?

The initial step in Fig. 1, phylloxera invasion of roots and development of feeding sites on the mature roots can be prevented by successful quarantine, if phylloxera are not yet present. In most parts of the viticultural world, however, phylloxera are present.

To be successful the mobile, first instar phylloxera need to identify the grape roots as a potential host and initiate galling. Recognition modalities are probably chemical; root constituents, root exudates, or volatiles might be involved in identification of hosts. Physical damage and plant hormone analogues secreted from salivary glands might be used by the plant to initiate feeding site galls. If we understood these processes could we use this knowledge to disrupt them through manipulation of vine physiology or soil chemistry? Insecticides tend not to be predictably effective for phylloxera control, especially in heavy soils, because of problems with distribution and stability. Could we solve these problems with downwardly mobile systemic insecticides, were some to be developed? If the current resistance mechanisms of American *Vitis* were to fail, could we find other resistance mechanisms in nature? In this age of genetic engineering, production of non-natural rootstocks also might be possible. Would the use of chemicals that stimulated induced host plant resistance (Omer *et al.*, 2000) prevent field populations from building?

The next step in the process is invasion and infection by fungal pathogens. We do not understand the ecology of this process well. The surfaces of new roots become infected with an array of fungi, including beneficial mycorrhizal species. If there is a competition for infection sites between pathogenic and non pathogenic fungi, could we alter the soil environment to favor the non pathogenic forms? Would use of large amounts of organic matter select for detritivory at the expense of pathogenicity? Would fungicides to control phylloxera damage be useful? Would soil amendments to increase the number and type of beneficial soil microbes help? Answers to these questions will require carefully conceived, replicated and well controlled experiments.

The next step is the girdling of the roots by the pathogens to kill the roots. Can we slow this process by stimulating acquired systemic resistance? Stresses influence vine defenses against pathogens and preliminary data suggest that water-stress increases the virulence of fungal isolates to vine roots. If this finding is confirmed, can we predict that alleviating vine stress by irrigation, fertilization, and limiting crop load will decrease vine damage?

It should be recognized that vineyards on strongly resistant rootstocks have a finite lifespan. In California vineyards tend to last 20 to 30 years even without phylloxera damage. If it takes 5-10 years for a phylloxera infestation to become established in a newly infested vineyard, and if we mitigate damage so that rather than dying in 3-5 years the vineyards die in 6-10 years, all-or-nothing phylloxera control may not be necessary, and an incremental approach may be minimally acceptable.

4 CONCLUSION

Development of any of these management options is a long term challenge that will take considerable research resources. Can expenditure of those resources be justified? We have an enigma. The best measure of phylloxera virulence is field performance of rootstocks, and there is no field evidence that they are failing. On the other hand, bioassays results have detected increasing phylloxera virulence, though it is not yet to a level that is expressed in the field.

We leave the question unanswered for this conference. But we cannot leave phylloxera research with this question unanswered. We see this as a primary phylloxera challenge for the next decade.

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