Vitis **36** (4), 199–205 (1997)

Population dynamics of grape phylloxera in California vineyards

by

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S u m m a r y : Field monitoring was conducted to investigate population growth of grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), in commercial grapevines in California. Phylloxera populations started from very low densities each spring, they increased exponentially and peaked during mid-summer, and then declined from mid- to late-summer. A second population peak was observed in the fall. Populations increased and declined simultaneously across all age classes. Egg populations were highest, followed by 1st and 2nd, and then 3rd and 4th instars; adult populations were the lowest. The distribution of age classes as a proportion of the total population indicated a higher intrinsic rate of increase in field vines in spring and early summer than was observed in the laboratory. Densities of phylloxera on tuberosities were highest during the summer and coincided with the population maximum. Densities of phylloxera on nodosities were highest in early spring and in the fall and coincided with periods of root flush. Evaluation of the relationship of soil temperatures to developing phylloxera suggested that decline of phylloxera populations in mid- and late-summer cannot be attributed to temperatures below a developmental threshold. Decreased root quality or quantity and mortality factors may explain this decline. Phylloxera overwintered as 1st or 2nd instars. Analysis of spatial distribution of phylloxera using Taylor's power law and Iwao's patchiness regression indicated that phylloxera populations are aggregated. The significance of this research with respect to phylloxera management is discussed.

K e y w o r d s : grape phylloxera, Daktulosphaira vitifoliae, grapevines, population, growth, distribution.

Introduction

Grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), is a debilitating pest of grapevines. Under greenhouse conditions phylloxera feeding provides avenues for infections by opportunistic fungi that promote root decline; in vineyards the infections also are associated with phylloxera (DAVIDSON and NOUGARET 1921; OMER *et al.* 1995 b; GRANETT *et al.* 1998). Phylloxera damage is minimized commercially by the use of phylloxera-resistant rootstocks which have been successful for more than a century. Laboratory bioassays and field observations have documented variability of phylloxera with regard to utilization of different *Vitis* cultivars (BÖRNER 1914; STEVENSON 1964; KING and RILLING 1985; GRANETT *et al.* 1987; DE BENEDICTIS and GRANETT 1992; GRANETT *et al.* 1992; DE BENEDICTIS *et al.* 1996) and DNA analyses of phylloxera have documented genetic variability (FONG *et al.* 1995). Because of selective adaptations to particular rootstocks, strains of phylloxera may become damaging in vineyards (GRANETT *et al.* 1985; SONG and GRANETT 1990; HIRSCHMANN and SCHLAMP 1994). Insecticides and other control measures have been used to prevent phylloxera damage, but none has proven as effective as resistant rootstocks (GRANETT *et al.* 1997).

Reports from laboratory (GRANETT *et al.* 1983; GRANETT and TIMPER 1987), and greenhouse experiments (DE KLERK 1974; KING and RILLING 1985) suggest that phylloxera populations grow exponentially when grape hosts and soil temperatures are favorable. In experiments with excised roots OMER *et al.* (1995 a) demonstrated that preformed root swellings allow phylloxera populations to develop more rapidly than they do on previously uninfested roots. Field studies have demonstrated that phylloxera populations develop better in clay soil than sandy soil. Each fall populations plummet and the insect overwinters as a 1st instar hibernant with substantial overwintering mortality (DAVIDSON and NOUGARET 1921; STEVENSON 1964; BUCHANAN 1990; CONELLY 1995). HELM *et al.* (1991) suggested that soil moisture is inhibitory toward high populations and that dry conditions favor population growth. HELM *et al.* (1991) and CONNELLY (1995) presented data showing population minima during summer, at times when population decline could not be attributed to cold temperatures. CONNELLY's explanation of these minima was that they are either inter-generational periods of time or are due to extrinsic factors.

Despite these studies on phylloxera biology and development, little is known about phylloxera population dynamics in the field. Quantitative knowledge of phylloxera populations is needed to understand spread rates of phylloxera and grapevine damage, cultural limitations of spread and phylloxera mortality factors. Such knowledge is essential for development of management strategies and evaluation of effectiveness of tactics which might be used to control phylloxera. In this research, we characterize phylloxera population dynamics on mature roots and on newly growing rootlets in California vineyards. We describe

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population growth and densities of each life stage of phylloxera seasonally. We also analyze the spatial distribution of phylloxera populations in the vineyard.

Materials and methods

Phylloxera populations were studied in two viticultural regions of California. The first vineyard planted with own-rooted *Vitis vinifera* L. cv. Chardonnay grapevines is near Stockton, San Joaquin Co., in the Central Valley which is a warm region. This vineyard was irrigated heavily (about 40 l/vine per week in May and 120 l/vine per week from June through September) and fertilized regularly by the farmer in an attempt to counteract the effects of phylloxera during both years of the study, 1995 and 1996. The second vineyard had *V. vinifera* Gewürztraminer scion planted on AXR#1 rootstock (=Ganzin-1 or ARG1, a *V. vinifera* L. x *V. rupestris* Scheele hybrid) is near Ukiah, Mendocino Co., in the cooler north coast viticultural region. During the study this vineyard was irrigated 12 July, 20 September and 4 October, 1996.

Populations were monitored by sampling randomly selected grapevines at 3-week intervals from May through November and once in February. On each sampling date, 20 root samples were extracted from near vine trunks from soil volumes of ca. 0.3 m^3. Grape roots were placed in plastic bags, transported to the laboratory in an ice chest, and inspected with a microscope for phylloxera populations. Numbers of phylloxera eggs, nymphs of each instar and adults associated with swellings on mature roots (tuberosities) or swellings on newly growing rootlets (nodosities) were recorded. Nymphal instar of each immature was assessed by size (DAVIDSON and NOUGARET 1921) and for purposes of analyses we combined densities of 1st and 2nd instars as well as densities of 3rd and 4th instars. Dry weights of root samples were determined. Phylloxera population densities were expressed as numbers of phylloxera/g dry root weight. At each sampling date, soil temperatures were measured at 10, 15, and 25 cm deep using thermister probes. We evaluated the 3 depths, to phylloxera populations.

One-way analysis of variance (ANOVA) (PROC GLM, SAS INSTITUTE 1989) was used to compare mean densities of phylloxera age classes on nodosities and tuberosities across sampling dates. Densities were transformed by

$$\sqrt{(x + 0.5)}$$

to correct for heterogeneity of variance before conducting the statistical analyses. Means separation was made by DUNCAN's (1955) multiple range tests at $\alpha = 0.05$.

Laboratory data of GRANETT *et al.* (1983) were reanalyzed to determine the age distribution of phylloxera feeding on Cabernet Sauvignon tuberosities and nodosites using the methods of CAREY (1983, 1993). The proportions of the population in the egg, immature and adult stages were calculated using r (intrinsic rate of increase) values from GRANETT *et al.* (1983) as well as hypothetical r values. Distributions from laboratory data were compared with the distributions observed in the vineyards.

Data collected over two years from the Stockton vineyard were used to investigate the spatial distribution of infestations. Because 1st and 2nd instars were present throughout our sampling, their combined densities were used to estimate the spatial distribution. The mean density (x) and variance (s^2) per sampling date were calculated and used in the analysis. Taylor's power law (TAYLOR 1961) and IWAO's patchiness regression (IWAO 1968) were used to analyze the spatial distribution of grape phylloxera. Taylor's power law relates the variance (s^2) to the mean (x) by $s^2 = ax^b$. To estimate a and b, the values of $\ln(s^2)$ were regressed against those of $\ln(x)$ using the model

$$\ln(s^2) = \ln(a) + b\ln(x) .$$

The slope (b) indicates a uniform, random, and aggregated distribution when $b < 1$, $b = 1$ and $b > 1$, respectively. Data were analyzed with PROC REG (SAS INSTITUTE 1989). The hypothesis, H_0: $b = 1$, was analyzed using a t-test (SOKAL and ROHLF 1981).

Iwao's patchiness regression method quantifies the relationship between LLOYD's (1967) mean crowding index (m) and sample mean density (x) by

$$m = \alpha + \beta x ,$$

where m is determined as $[x + (s^2/x - 1)]$. The values of α and β were estimated by linear regression of m on x. The slope (β) indicates the distribution pattern ($\beta < 1$, uniform; $\beta = 1$, random; $\beta > 1$, aggregated). Data were analyzed with PROC REG (SAS INSTITUTE 1989). The hypothesis, H_0: $\beta = 1$, was analyzed using a t-test (SOKAL and ROHLF 1981).

Results

Densities of grape phylloxera sampled from the Stockton vineyard (Fig. 1) were low in spring and increased exponentially through mid-summer when populations began to decline. A second population peak occurred in fall 1996 but this second peak was seen only as a shoulder on the downward summer slope in the 1995 data. By November in both years, populations attained their lowest densities and

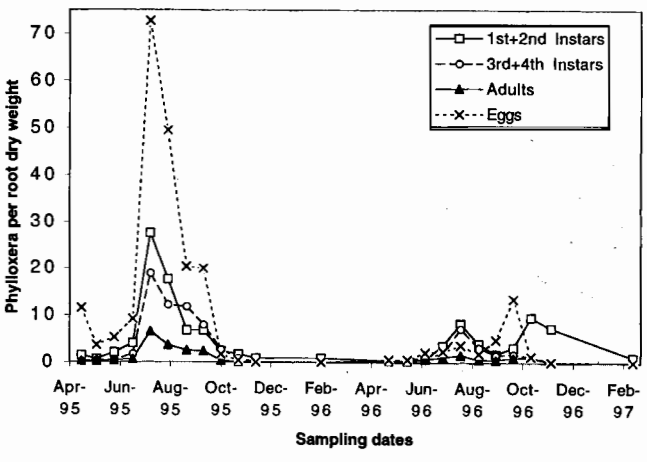


Fig. 1: Populations of grape phylloxera at a Stockton, CA, own-rooted Chardonnay vineyard by stage of life cycle.

only 1st or 2nd instar phylloxera were present. Densities (mean ± SEM phylloxera/g dry root weight) at peak abundance in the first season were 72.7 ± 17.7 for eggs, 27.7 ± 6.0 for 1st and 2nd instars, 18.9 ± 5.2 for 3rd and 4th instars, and 6.5 ± 1.7 for the adults and these peaks all occurred on the same sampling date (26 July, 1995). In the second year, densities for the summer peak abundance (30 July, 1996) were 3.6 ± 0.9 for the eggs, 8.2 ± 2.0 for 1st and 2nd instars, 7.2 ± 1.6 for 3rd and 4th instars, and 1.6 ± 0.3 for adults. Phylloxera populations exhibited a second peak in early fall (between 1 and 22 October, 1996). During winter, densities of 1st and 2nd instars were 0.8 ± 0.4 in the first year (15 February, 1996) and 1.0 ± 0.3 in the second year (20 February, 1997). Neither adults nor 3rd and 4th instars were found during winter in either year.

Populations of grape phylloxera in the Ukiah vineyard (Fig. 2) exhibited two population peaks (31 July, 1996 and 11 September, 1996). Egg densities were not as high as densities of the 1st and 2nd instars but tended to exceed densities of the more developed forms (3rd and 4th instars and adults). Densities for the first population peak were 7.4 ± 1.9 for the eggs, 6.9 ± 1.8 for 1st and 2nd instars, 3.8 ± 0.9 for 3rd and 4th instars, and 0.8 ± 0.2 for adults. For the second peak, densities were 8.2 ± 4.2 for the eggs, 32.6 ± 15.8 for 1st and 2nd instars, 6.7 ± 4.1 for 3rd and 4th instars, and 5.1 ± 3.3 for adults. By November and through the winter, the population consisted of 1st or 2nd instars. In winter, densities of 1st or 2nd instars were 0.4 ± 0.1. At Ukiah phylloxera were more abundant during the second peak than the first.

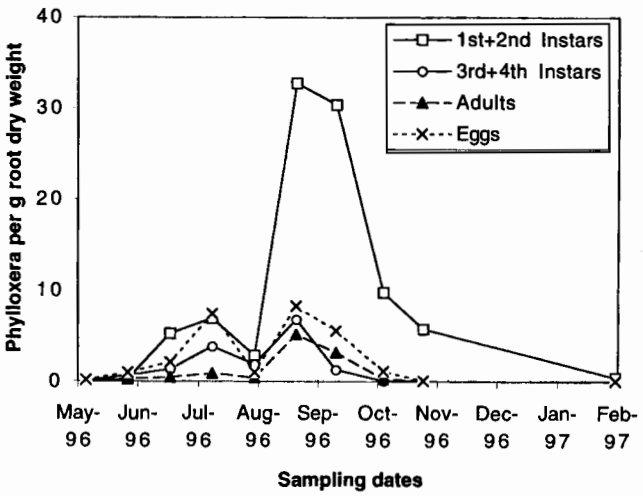


Fig. 2: Populations of grape phylloxera at a Ukiah, CA, vineyard on AXR#1 rootstock by stage of life cycle.

In Stockton, densities of phylloxera established on nodosities and tuberosities in 1995 were greater than the densities in 1996 but timing of maxima were similar (Fig. 3). The ANOVA indicated that densities of phylloxera on tuberosities during the summer were significantly higher than on nodosities ($P<0.001$) but not during early spring and the fall ($P>0.126$). Densities of phylloxera on tuberosities had a single peak each year during the summer coinciding with the yearly peaks in the total population (35.5 ± 9.7 in 1995 and 11.4 ± 3.0 in 1996). Densities of phylloxera on nodosities had two yearly peaks, one in the summer and a second in the fall. These densities were lower than the peaks

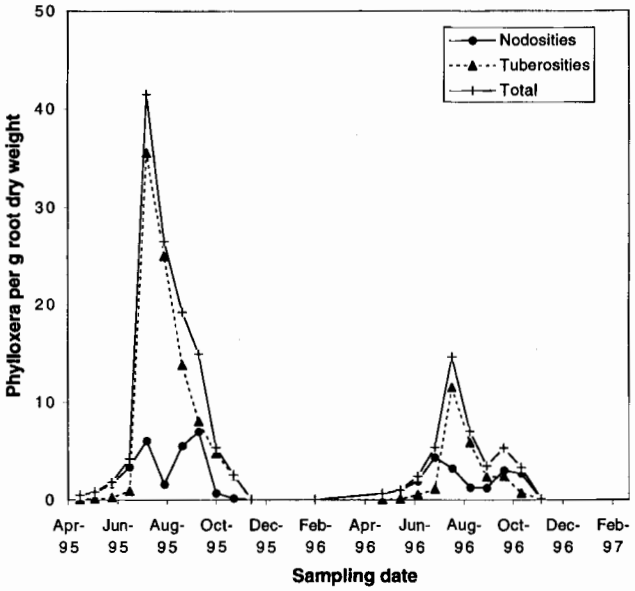


Fig. 3: Grape phylloxera populations on nodosities and tuberosities at a Stockton, CA, own-rooted Chardonnay vineyard.

for tuberosities and were 6.0 ± 1.7 and 6.9 ± 2.5 for 1995 and 3.2 ± 0.6 and 3.3 ± 1.2 for 1996. In Ukiah, there was a double peak for both nodosities and tuberosities with the tuberosity populations being the higher of the two for both peaks (Fig. 4). Densities of phylloxera on tuberosities during the summer were significantly higher than on nodosities ($P<0.001$). Tuberosity maxima were 3.9 ± 1.0 and 10.4 ± 7.4; nodosity maxima were 1.1 ± 0.4 and 1.5 ± 0.8. The first nodosity peak predated the first tuberosity peak by one sampling period. In both vineyards the nodosity populations began to grow in the spring prior to the tuberosity populations.

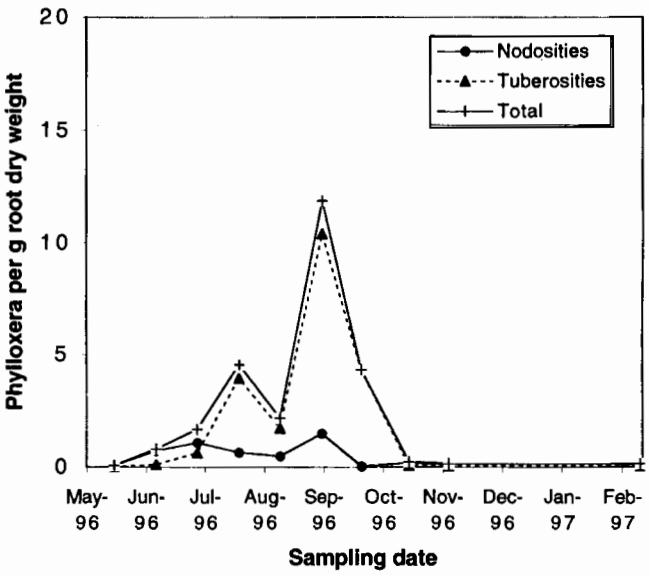
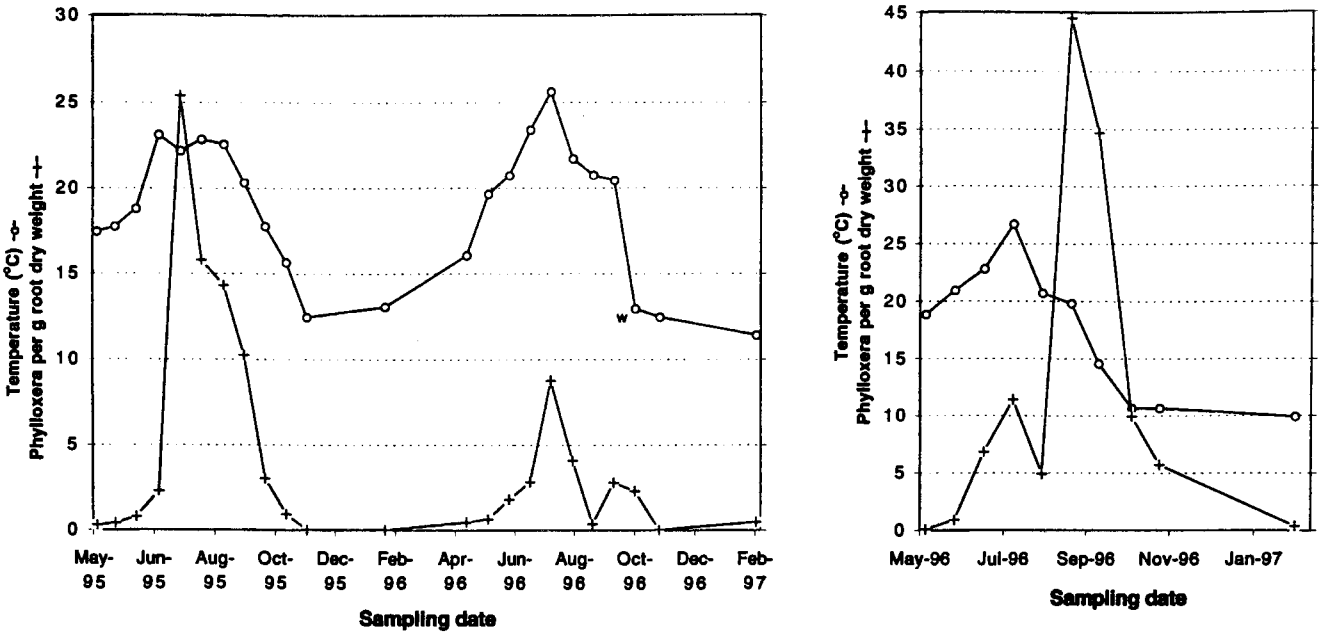


Fig. 4: Grape phylloxera populations on nodosities and tuberosities at a Ukiah, CA, vineyard on AXR#1 rootstock.

The relationships of developing phylloxera to soil temperature in the two vineyards are shown in Figs. 5 and 6. Phylloxera populations increased as temperature increased during spring and early summer. In both vineyards, the summer phylloxera populations began to fall after the temperature exceeded 23 °C and prior to the time when temperatures dropped below 18 °C.



Figs. 5 and 6: Relationship of developing phylloxera to soil temperatures at a Stockton, CA, own-rooted Chardonnay vineyard (Fig. 5, left) and at a Ukiah, CA, vineyard on AXR#1 rootstock (Fig. 6, right).

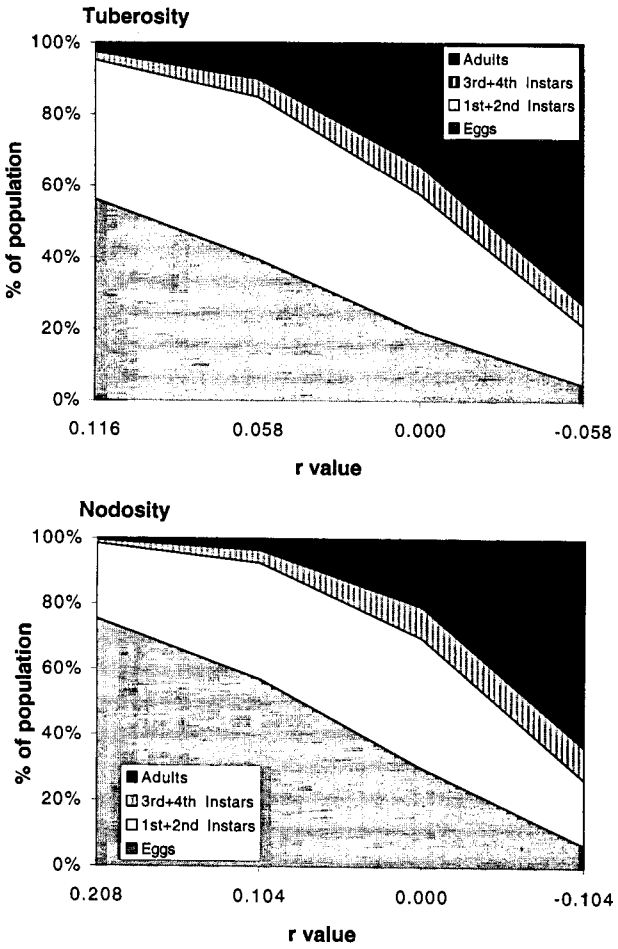


Fig. 7: Stable age distributions for phylloxera growing on Cabernet Sauvignon root pieces as calculated from the data of GRANETT *et al.* (1983) using the methods of CAREY (1984, 1993). Values for r plotted are double the r value reported for the laboratory data, and two intervals below. Distributions for tuberosity and nodosity insects were calculated separately.

We determined the proportions of phylloxera in each age class by extrapolating from observed and hypothetical r values (Fig. 7). The r values chosen spanned the range from twice the value calculated in GRANETT *et al.* (1983) to a negative r value equal in absolute magnitude to the measured r. The underlying assumption is that differences in r values in laboratory data are due to differences in fecundity and not in age-specific mortality. The stable age distributions for tuberosity and nodosity phylloxera were similar in trend: the proportion of eggs generally decreased as the r value decreased and the proportion of adults tended to increase. For the lower r values plotted, the proportion of eggs was greater for nodosities than tuberosities and the proportion of adults was greater for tuberosities than nodosities.

The proportions in each age class varied seasonally in vineyards (Fig. 8). In May, the distributions in both vineyards and years tended to be dominated by eggs and the proportion of eggs decreased as the populations progressed toward the fall, with several exceptions. One exception occurred in Ukiah where a temporary spike in the proportion of eggs occurred in July with the sampling after a vineyard irrigation. In Stockton, 1996 a large proportion of eggs was seen in September at the time of the fall root flush. The proportion of immatures tended to be inversely related to the proportion of eggs in the population. The proportion of adults either was constant or decreased during the year. The young immatures were the only individuals found during the February samplings.

Analysis of spatial distribution of phylloxera using Taylor's power law and Iwao's patchiness regression yielded significant regression lines (Fig. 9). Taylor's power law fit the data better, yielding a higher value of r^2 than Iwao's patchiness regression. Slopes from both models (b and β) were significantly greater than 1 ($P<0.001$, $n = 25$), indicating an aggregated spatial distribution.

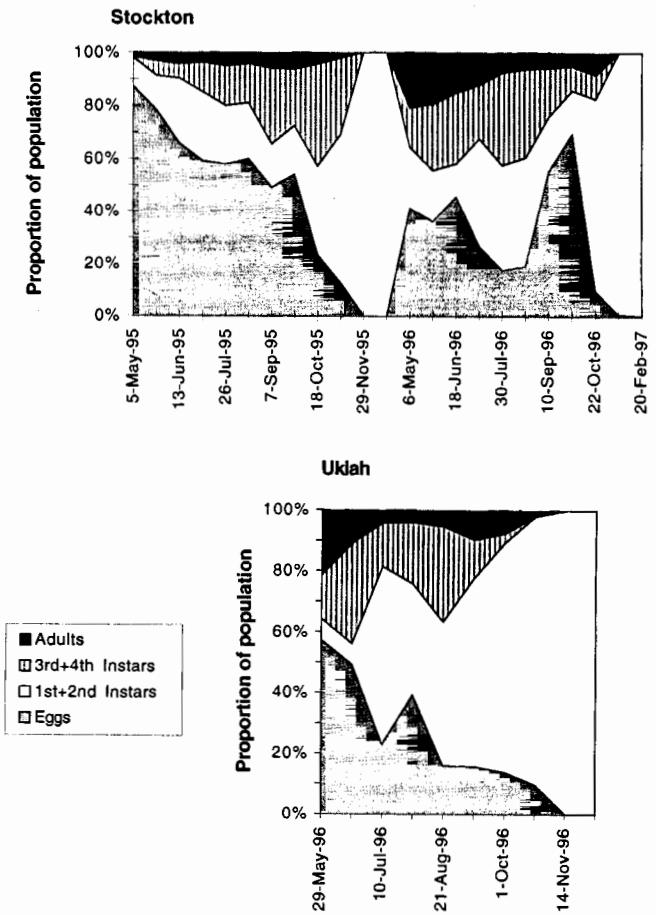


Fig. 8: Distribution of egg, immature and adult age classes at a Stockton, CA, own-rooted Chardonnay vineyard and a Ukiah, CA, vineyard on AXR#1 rootstock as proportions of the population.

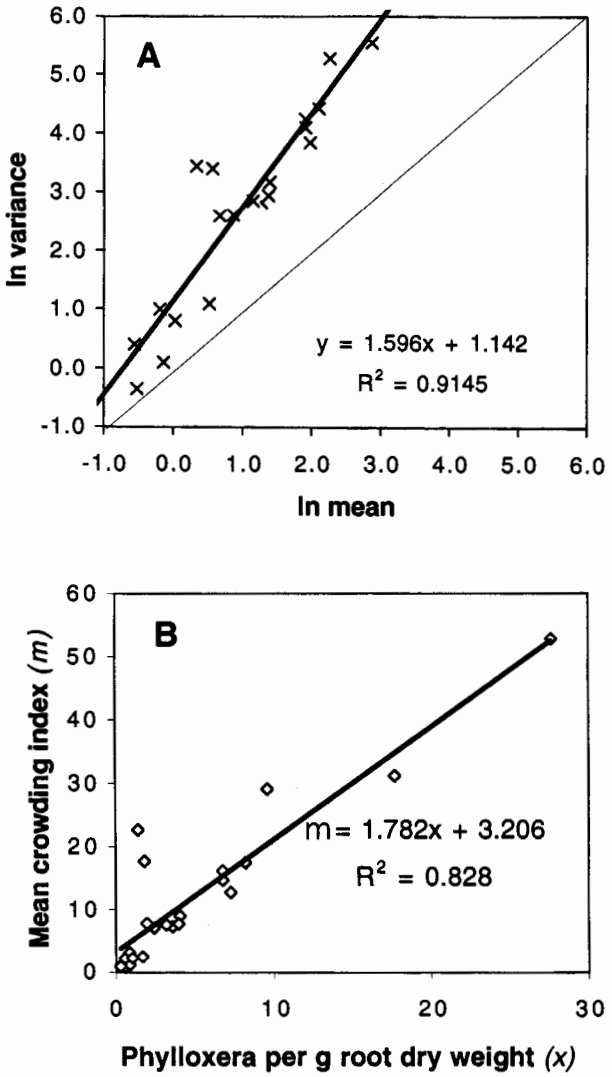


Fig. 9: Distribution analysis. (**A**) Taylor's power law: ln variance = 1.14 + 1.60 ln mean, $r^2 = 0.91$; (**B**) Iwao's patchiness regression: $m = 3.21 + 1.78\,x$, $r^2 = 0.83$.

Discussion

CONNELLY (1995) raised the question of whether population maxima and minima in Oregon vineyards were due to sequential, synchronized phylloxera generations or to extrinsic factors or both. We believe for several reasons that extrinsic factors are the more likely cause. First, egg laying can occur during about 60 % of the insect's life (GRANETT *et al.* 1983). Since eggs hatch in less than a week, overlap of generations would occur soon after the first generation. Second, to a large extent in the Oregon data as well as in our data, the population peaks occur for different life stages simultaneously. If generational development were the cause of population maxima and minima, we would expect that maxima and minima of subsequent developmental stages to be temporally offset because of developmental time. But they were not. Third, it is unlikely that generations would be synchronized because temperature varies in the soil by depth. Since phylloxera development is influenced by temperature (GRANETT and TIMPER 1987; BELCARI and ANTONELLI 1989; CONNELLY 1995; TURLEY *et al.* 1996) the insect would not develop at equal rates at different depths and so synchrony would be absent.

Extrinsic factors which may account for the observed population dynamics and age distributions include temperature, quality and quantity of roots, and the activity of soil-inhabiting pathogens of phylloxera. Laboratory experiments show that temperature must exceed 18 °C for phylloxera to establish feeding sites (TURLEY *et al.* 1996). Population doubling times between 21 and 28 °C varied between 4.7 and 7.6 d and overlapped (GRANETT and TIMPER 1987). Therefore, we would predict that populations in the field would begin to grow in spring as temperature exceeded the 18 °C threshold, grow steadily through the summer, crest in fall as temperatures decline below the 18 °C threshold then drop rapidly with temperature. STEVENSON (1964) observed this pattern of phylloxera development in Ontario, Canada with vine roots that only supported nodosities. Our observations for California vineyards suggest a different pattern. The phylloxera population began to grow exponentially in spring as temperatures became favorable. However, it crested with a mid-summer peak and began to decline at both locations while temperatures remained favorable (Figs. 5 and 6). Therefore this summer peak and drop cannot have a temperature-related explanation. The

second population peak at both locations occurred in fall and the decline from that peak would be consistent with a hypothesis that low temperature was responsible.

A second explanation for population decline is a change in root quality or quantity. The summer population rose exponentially in May and June and crested at approximately the same dates each year, in both locations suggesting that these trends are related to seasonally controlled changes in vine physiology or root availability. The proportions of insects in each age class (Fig. 8) also shed light on the cause of population changes. The proportion of eggs in May and June is consistent with r values that are higher than the r value observed for the laboratory data (Fig. 7, 0.058 for tuberosities and 0.104 for nodosities). Because a high r value implies a high level of nutrition, the vineyard data suggest that nutritional quality of the roots is high in the spring and decreases steadily as the season progresses. In addition, GRANETT *et al.* (1998) suggest that root death caused by phylloxera galling and plant pathogenic fungi are maximal during mid-summer, and this root loss may account for some of the decline in phylloxera populations.

A third explanation is activity of an extrinsic mortality factor. Laboratory data that assumed no extrinsic mortality factors present showed that as r decreases the proportion of eggs in the population decreases and the proportion of adults correspondingly increases (Fig. 7). Yet in the field, the proportion of the populations that were adults at each sampling date was not inversely related to the proportion of eggs. The adults remained at the same proportion in the population from May through September or declined. The pattern seen in the vineyard is consistent with a hypothesis of limited development to the adult stage or a mortality factor that affects some or all of the life stages before the adult stage (CAREY 1984). Mortality of immatures may be a function of a pathogenic agent or may simply be a result of the deterioration of the plant tissues upon which the phylloxera feed.

Continued research on the interactions of vine physiology, soil ecology and insect and plant pathology with phylloxera populations is needed to test the hypotheses that nutritional and pathogenic factors are involved. Mechanistic explanations are important because they may contribute to the development of curative or prophylactic tools for control of phylloxera populations and damage to vines.

HELM *et al.* (1991) suggested that dry vineyard conditions are associated with phylloxera outbreaks and wet conditions are associated with lower phylloxera populations. Explanations that invoke the activity of fungi would suggest different population dynamics in wet and dry vineyards. Fungi often require warm, moist soil conditions to be optimally active and might tend to decrease phylloxera populations when these conditions were met. It is necessary to test this hypothesis directly under vineyard conditions. Contrary to the interpretation of HELM *et al.* (1991), wet conditions on their own are not sufficient to prevent phylloxera outbreaks or damage to susceptible vines. The Stockton vineyard described in our work was under regular drip irrigation through 1995 and 1996 and yet experienced high populations and vine decline.

Our data suggest that nodosities and tuberosities serve very different roles in population growth in vineyards. Nodosities by definition develop on immature roots which are generated twice during the year (WOLPERT 1992). The spring root flush coincides with the first increase of phylloxera populations on nodosities. Tuberosities begin to develop only after the population growth on nodosities (Figs. 3 and 4). However, phylloxera populations on tuberosities frequently exceed those seen on nodosities. The fall population peaks occur primarily on rootlets and most of the individuals are 1st or 2nd instars and become hibernants or die prior to winter. The fall root-flush therefore would tend to increase the number of phylloxera becoming quiescent and overwintering. Although we observed the high overwintering mortality (Figs. 1 and 2) mentioned by DAVIDSON and NOUGARET (1921) and STEVENSON (1964), we do not know whether a strong fall root-flush would increase overwintering success or not. This question has practical implications: fertilization of vineyards in the fall should increase the root-flush and thereby improve vine health the following season; the increase in phylloxera populations that occurs with such management might have an inverse impact on vine health.

Aggregated populations are characteristic of phylloxera (Figs. 7 and 8). OMER *et al.* (1995 b) found that phylloxera are attracted to and develop more rapidly on preformed tuberosities under laboratory conditions, and therefore appear aggregated. Our data demonstrate this tendency under field conditions. This aggregation would imply that phylloxera population growth rate is higher for large populations than for small populations because large populations can take better advantage of the prevalence of preformed tuberosities. This may explain the long lag-time prior to phylloxera population growth sometimes observed in newly infested vineyards and rapid decline of some highly infested vineyards.

Management of phylloxera by use of resistant rootstock is limited by costs of replanting as well as by the development of aggressive strains. Our data suggest that there may be physiological, ecological or pathological factors that limit phylloxera population growth naturally in *V. vinifera*- and AXR#1-rooted vineyards. Managing these factors may allow farmers to delay replanting infested vineyards. These alternative mortality factors also may help delay field selection of aggressive strains by decreasing the fitness benefit afforded such strains in rootstock fields. A more in-depth understanding of which factors are involved and their limitations is needed before integrated pest management for phylloxera can be developed.

Acknowledgements

We wish to thank L. KOCSIS (Fulbright scholar visiting the University of California, Davis from his home institution, Pannon University of Agricultural Sciences, Georgikon Faculty of Agronomy, Keszthely, Hungary), J. R. CAREY, P. PESSERAU and D. LOTTER (University of California, Davis) for assistance with this work and criticism of the manuscript. We thank F. RODRIGUEZ (Vineyard Properties Corp.) and M. BOER (Mendocino Vineyard Co.) for assistance

and access to vineyards. This research was partially supported by the American Vineyard Foundation, a specific cooperative agreement with the USDA (Horticultural Crops Research Laboratory, Fresno, California), and ProGuard, Inc. (Suisun, California).

References

Belcari, A.; Antonelli, R.; 1989: The influence of temperature on the development of pre-imaginal stages of *Viteus vitifoliae* (Fitch)(Rhynchota-Phylloxeridae). 3. Duration of larval development in epigeous generations at constant temperatures. In: Cavalloro, R. (Ed.): Influence of Environmental Factors on the Control of Grape Pests, Diseases and Weeds. Meeting of the EC Experts' Group, 6-8 October 1987, Thessaloniki, 115-124. A. A. Balkema, Rotterdam.

Börner, C.; 1914: Über reblausanfällige und -immune Reben. Biologische Eigenheiten der Lothringer Reblaus. Biologisches Zentralblatt **34**, 1-8.

Buchanan, G. A.; 1990: The distribution, biology and control of grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), in Victoria. La Trobe. Ph. D. Diss. Univ. Bundoora, Victoria, Australia.

Carey, J. R.; 1983: Practical application of the stable age distribution: Analysis of a Tetranychid mite (Acari: Tetranychidae) population outbreak. Environ. Entomol. **12**, 10-18.

- -; 1984: Demographic determinants of stage composition in Tetranychid mite populations. In: Griffiths, D. A.; Bowman, C. E. (Eds.): Acarology VI, Vol. I, 609-616. John Wiley & Sons, NY.

- -; 1993: Applied Demography for Biologists with Special Emphasis on Insects. Oxford Univ. Press, New York.

Connelly, A. E.; 1995: Biology and demography of grape phylloxera, *Daktulosphaira vitifoliae* (Fitch) (Homoptera: Phylloxeridae), in Western Oregon. MS Thesis, Oregon State Univ.

Davidson, W. M.; Nougaret, R. L.; 1921: The grape phylloxera in California. U. S. Dep. Agric. Bull. **903**.

De Benedictis, J. A.; Granett, J; 1992: Variability of responses of grape phylloxera (Homoptera: Phylloxeridae) to bioassays that discriminate between California biotypes. J. Econ. Entomol. **85**, 1527-1534.

- -; - -; Taormino, S. T.; 1996: Differences in host utilization by California strains of grape phylloxera. Amer. J. Enol. Viticult. **47**, 373-379.

De Klerk, C. A.; 1974: Biology of *Phylloxera vitifoliae* (Fitch) (Homoptera: Phylloxeridae) in South Africa. Phytopathologica **6**, 109-118.

Duncan, D. B.; 1955: Multiple range and multiple *F* tests. Biometrics **11**, 1-42.

Fong, G.; Walker, M. A.; Granett, J.; 1995: RAPD assessment of California phylloxera diversity. Molec. Ecol. **4**, 495-464.

Granett, J.; Bisabri-Ershadi, B.; Carey, J.; 1983: Life tables of phylloxera on resistant and susceptible grape rootstocks. Entomol. Exp. Appl. **34**, 13-19.

- -; Boubals, D.; Walker; M. A.; De Benedictis, J. A.; 1997: Grape phylloxera. In: Wilson, L. T.; Dennehy, T. J.; Bostanian, N. J. (Eds.): Arthropod and Nematode Management in Vineyards with Emphasis on North America and Western Europe. Pergamon, New York (in press).

- -; De Benedictis, J. A.; Marston, J.; 1992: Host suitability of *Vitis californica* Bentham to grape phylloxera, *Daktulosphaira vitifoliae* (Fitch). Amer. J. Enol. Viticult. **43**, 249-252.

- -; Goheen, A. C.; Lider, L. A.; White, J. J.; 1987: Evaluation of grape rootstocks for resistance to type A and type B grape phylloxera. Amer. J. Enol. Viticult. **38**, 298-300.

- -; Omer, A. D., Pessereau, P.; Walker, M. A.; 1998: Fungal infections of grapevine roots in phylloxera-infested vineyards. Vitis, companion paper submitted for publication.

- -; Timper, P.; 1987: Demography of grape phylloxera (*Daktulosphaira vitifoliae* (Fitch) (Homoptera: Phylloxeridae), at different temperatures. J. Econ. Entomol. **80**, 327-329.

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

Helm, K. F.; Readyshaw, J. L.; Cambourne, B.; 1991: The effect of drought on populations of grape phylloxera in Australian vineyards. Wine Ind. J. **1991**, 194-200.

Hirschmann, J.; Schlamp, W.; 1994: Alter Schädling, neuer Ärger. Weinbauamt mit Weinbauschule Eltville. Wiesbaden.

Iwao, S.; 1968: A new regression method for analyzing the aggregation pattern of animal populations. Res. Popul. Ecol. **10**, 1-20.

King, P. D.; Rilling, G.; 1985: Variations in the galling reaction of grapevines: Evidence of phylloxera biotypes and clonal reaction to phylloxera. Vitis **24**, 32-42.

Lloyd, M.; 1967: Mean crowding. J. Anim. Ecol. **36**, 1-30.

Omer, A. D.; De Benedictis, J. A.; Granett, J.; 1995 a: Grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), population response to preformed tuberosities. J. Appl. Entomol. **119**, 653-657.

- -; Granett, J.; De Benedictis, J. A.; Walker, M. A.; 1995 b: Effects of fungal root infections on the vigor of grapevines infested by root- feeding grape phylloxera. Vitis **34**, 165-170.

SAS Institute Inc.; 1989: SAS/STAT Users Guide, version 6, 4th ed. SAS Institute Inc., Cary, NC, USA.

Sokal, R. R.; Rohlf, F. J.; 1981: Biometry, 2nd ed. Freeman, San Francisco, California.

Song, G. C.; Granett, J.; 1990: Grape phylloxera (Homoptera: Phylloxeridae) biotypes in France. J. Econ. Entomol. **83**, 489-493.

Stevenson, A. B.; 1964: Seasonal history of root-infesting *Phylloxera vitifoliae* (Fitch) (Homoptera: Phylloxeridae) in Ontario. Can. Entomol. **96**, 979-987.

Taylor, L. R.; 1961: Aggregation, variance and the mean. Nature (London) **189**, 732-735.

Turley, M.; Granett, J.; Omer, A. D.; De Benedictis, J. A.; 1996: Grape phylloxera (*Homoptera: Phylloxeridae*) temperature threshold for establishment of feeding sites and degree-day calculations. Environ. Entomol. **25**, 842-847.

Wolpert, J. A.; 1992: General viticulture. In: Flaherty, D. L.; Christensen, L. P.; Lanini, W. T.; Marois, J. J.; Phillips, P. A.; Wilson,L. T. (Eds.): Grape Pest Management, 2nd ed., Publication 3343. Univ. California, Division of Agriculture and Natural Resources, Oakland, California.

Received July 29, 1997