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Populations of grape phylloxera gallicoles on rootstock foliage in Hungary

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Summary

Populations of gallicole grape phylloxera (*Daktulosphaira vitifoliae* Fitch) were monitored in Keszthely, Hungary from June through October 1998 on foliage of the *Vitis berlandieri* Planch. x *V. riparia* Michx. rootstock cultivar Teleki 5 C. Though population size peaked in August, leaves from June through September were equally supportive of gallicole development and egg production. Demography varied with leaf position on shoots with the leaf in the terminal position having the most immature populations. Leaves 5 through 7 from the shoot terminal had highest population densities and the highest egg production. Population densities correlated with gall densities. Populations on the rootstock cultivar Rupestris du Lot and *Vitis amurensis* Rupr. were low but populations were high on the rootstock cultivars 101-14 MGT, T. K. 5 BB and Fercal. However, magnitude of phylloxera eggs/adult on cultivars tested was not numerically distinguishable. High phylloxera population numbers were correlated with decreased vine productivity as measured by shoot growth.

Key words: grape phylloxera, *Daktulosphaira vitifoliae*, *Vitis*, gallicole, demography, populations.

Introduction

Grape phylloxera, *Daktulosphaira vitifoliae* (Fitch) gallicoles induce formation of leaf galls on some native American *Vitis* species and rootstocks derived from them. In addition, small numbers of phylloxera are found on the roots of such plants (Riley 1876, Davidson and Nougaret 1921). Induction of galls occurs on newly expanding leaves and once a leaf is fully expanded new galls cannot form (Rosen 1916). The galls and insects within persist after leaves have fully expanded. Hence, phylloxera population studies must quantify formation of galls and also insect survival, development and reproduction in the galls as the leaves age.

Population size of phylloxera gallicoles changes during the vine's growing season (Stevenson 1975). There has been a limited amount of population research in the form of gall counts (Stevenson 1966, 1970 a and b, 1975, Jubb 1977) but not on gallicoles within the galls. However, there is a clear linkage between populations on roots and gallicoles with regard to movement, genetics and feeding competence (Davidson and Nougaret 1921, Stevenson 1975, Hawthorne and Dennehy 1991, Kocsis *et al.* 1999). Therefore, better understanding of the gallicoles may shed light on the insect's capacity for damage and dispersal and limitations on overall population growth.

The objective of the present study was to determine the population dynamics of phylloxera gallicoles during the vine's seasons of growth.

Material and Methods

Study site: Studies were done in the rootstock nursery and garden of Veszprém University, Georgikon Faculty of Agronomy, Cserszegtomaj (near Keszthely), Hungary. The vineyard has had a long established phylloxera infestation and in addition, portions of the vineyard were infested by hand with phylloxera in 1990 (Kozma *et al.* 1997).

Seasonal prevalence of gallicoles on Teleki 5C: Six vines (each with 4-12 shoots) were randomly selected from a vine row at the beginning of the season. Previously unsampled shoots from the same set of 6 vines were evaluated at each of 4 sampling times at 5-week intervals, days of the year 177, 215, 252 and 286 (June, August, September and October, 1998 respectively). We removed leaves from positions 1, 3, 5, 7, 9, 11, 13 and 15 counting from the shoot terminal on each selected shoot, placed them in plastic bags and held them at 10 °C until evaluated. Because there were about 40-70 nodes on vine shoots by the end of this season, most odd numbered positions, were evaluated. The total number of immature and mature galls were counted on each selected leaf. We evaluated randomly up to 30 immature- and 30 mature galls per leaf and tallied their populations separately. Immature galls were characterized as being <2 mm in diameter and not being fully closed. We used a razor to open galls and then counted and classed the phylloxera by stage. Instar was estimated based on size (Davidson and Nougaret 1921). Newly hatched mobile nymphs (crawlers) were classed separately from the relatively immobile feeding nymphs.

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Eggs were counted and we combined the numbers for eggs and crawlers. These were combined because both are part of the next generation. The paucity of unhatched eggs in a gall after the adult dies (Granett and Kocsis, unpubl. observation) suggests that the proportion of eggs that hatch into crawlers capable of leaving the gall is very high. Therefore, whether the egg is hatched or unhatched is merely a matter of a few days and so by combining the numbers of eggs and crawlers, we get a better measure of the adults' fecundity. Adults were identified by the presence of eggs. The presence of other arthropods in galls was noted. In winter all canes of vines sampled were harvested and lengths measured. Cane length was regressed against cumulative phylloxera population size to determine influence of population on growth.

Gallicoles on different cultivars: We evaluated phylloxera gallicole numbers on the rootstock cultivars Fercal (*V. berlandieri* x *V. vinifera* L.), 101-14 MGT (*V. riparia* x *V. rupestris* Scheele), T. K. 5 BB (*V. berlandieri* x *V. riparia*), Teleki 5 C (*V. berlandieri* x *V. riparia*), Rupestris du Lot (*syn* St. George, *V. rupestris*). We also evaluated a selection of *V. amurensis* Rupr. For the rootstock cultivars, 4 replicate vineyard blocks each of 7 vines were randomly distributed in the vineyard area, however, with Rupestris du Lot one replicate was missing. For *V. amurensis* we had one block of 7 vines available. For each cultivar and replicate block we chose the most galled shoot for evaluation once on day 224 of the year. This date was chosen because phylloxera population size was apparently at its peak as suggested by the previously described Teleki 5 C experiment. We counted galls and gallicoles at leaf positions 1, 3, 5, 7, and 9 as previously described. Data for the Teleki 5 C experiment and the cultivar study were analyzed using one way analyses of variance (ANOVA) with date, leaf position and cultivar as the main effects. The dependent response variables were total number of feeding gallicoles plus eggs and crawlers per gall (total gallicoles), number of feeding immature gallicoles per gall, number of adult gallicoles per gall, number of eggs and crawlers per gall and number of eggs and crawlers per adult. Type III sum of squares were used. The least significant difference option was used to compare treatment effects using a value of $\alpha = 0.05$ (SPSS 1996).

Results

Seasonal prevalence of gallicoles on Teleki 5 C: Galls were present at all leaf positions on all sample dates except for position 15 from the shoot terminal, which had very few galled leaves (only 3 out of 24 observations) or galls. This position therefore could not be used for gallicole evaluations and was not considered in the statistical analyses.

Numbers of galls and total gallicoles per leaf, gallicoles of each stage per gall, and eggs and crawlers per adult on Teleki 5 C differed by date (Tab. 1). Gall numbers per leaf were highest for observations on day 215 but numbers for other observation dates did not differ from one another. Immatures plus adults per gall had the lowest counts on day 286 averaging fewer than one feeding insect per gall. For immature galls, the number of gallicoles per gall ranged from zero to 6. The number of feeding gallicoles in mature galls, ranged from zero to 24. Up to 4 adults were found in mature galls.

Mean numbers of eggs and crawlers per gall did not statistically differ from one another on the first three sampling dates; however, by the last sampling date the number of eggs was significantly lower (Tab. 1). The number of crawlers per gall rarely exceeded 10 % of the egg count. Eggs and crawlers per adult were lowest on day 286, with the day 252 counts being intermediate and the earlier season counts being high. Total gallicole number per leaf was highest on day 215 and declined thereafter (Tab. 1). The leaf average ranged up to 3,507 gallicoles including eggs. The mean gallicole population per shoot exceeded 45,000 gallicoles including eggs; the range was from 0 to <150,000.

Table 1

Gall and gallicole phylloxera population counts (mean ± SD) on grape rootstock leaves by day of year using data over all leaf positions. Counts were made on Teleki 5 C leaves collected from six rootstock vines in 1998

Day of year	Galls per leaf	Total gallicoles per leaf	Immatures per gall	Adults per gall	Eggs[a] per gall	Eggs[a] per adult
177	9 ± 37 b	172 ± 569 b	0.82 ± 0.26 a	0.54 ± 0.41 ab	58 ± 71 a	91 ± 77 a
215	73 ± 124 a	3,507 ± 8,863 a	1.22 ± 1.05 a	0.61 ± 0.43 ab	53 ± 63 a	80 ± 64 a
252	30 ± 57 ab	1,085 ± 2,706 ab	0.97 ± 0.40 a	0.67 ± 0.46 a	39 ± 45 a	55 ± 47 ab
286	31 ± 58 ab	222 ± 491 b	0.40 ± 0.32 b	0.35 ± 0.29 b	7 ± 8 b	28 ± 35 b
ANOVA*	F = 4.929 P = 0.003	F = 4.736 P = 0.003	F = 8.079 P = 0.000	F = 3.144 P = 0.029	F = 4.747 P = 0.004	F = 4.466 P = 0.006

[a] Tally for eggs includes crawlers (see text for explanation).

* The ANOVA had df = 3 for each of the dependent variables in the table with F and P values as shown.

Values in columns associated with different letters are statistically different from one another at $\alpha = 0.05$ by an LSD test.

Table 2

Gall and gallicole phylloxera population counts (mean ± SD) on grapes rootstock leaves by leaf position counting from the shoot terminal. Counts were made on Teleki 5 C leaves collected from six rootstock vines in 1998

Leaf position	Galls per leaf	Total gallicoles per leaf	Immatures per gall	Adults per gall	Eggs[a] per gall	Eggs[a] per adult
1	39 ± 67	235 ± 589	0.85 ± 0.36	0.27 ± 0.36 b	6 ± 8 c	23 ± 15 c
3	36 ± 73	385 ± 832	0.87 ± 0.41	0.44 ± 0.40 ab	12 ± 17 bc	37 ± 24 abc
5	40 ± 110	2,916 ± 10,146	0.79 ± 0.49	0.63 ± 0.35 a	42 ± 51 ab	55 ± 24 abc
7	36 ± 84	1,409 ± 3,290	0.83 ± 0.45	0.70 ± 0.38 a	70 ± 72 a	88 ± 73 ab
9	37 ± 72	1,827 ± 4,370	0.84 ± 0.67	0.59 ± 0.38 ab	67 ± 74 ab	94 ± 44 a
11	32 ± 72	1,001 ± 2,706	0.92 ± 1.55	0.55 ± 0.44 ab	32 ± 35 ab	55 ± 28 abc
13	18 ± 54	268 ± 1,019	0.96 ± 0.67	0.79 ± 0.62 ab	23 ± 29 abc	26 ± 29 bc
ANOVA*	F = 0.202 P = 0.976	F = 1.107 P = 0.361	F = 0.071 P = 0.999	F = 2.273 P = 0.044	F = 3.751 P = 0.002	F = 2.673 P = 0.022

[a] Tally for eggs includes crawlers (see text for explanation).
* The ANOVA had df = 6 for each of the dependent variables in the table with F and P values as shown.
Values in columns associated with different letters are statistically different from one another at $\alpha = 0.05$ by an LSD test.

Counts of galls and total gallicoles per leaf were statistically indistinguishable by leaf position (Tab. 2). The numbers for immatures per gall were also uniform and approached one per gall. The number of adults per gall was lowest at position 1 and was higher thereafter. The number of eggs and crawlers per gall was lowest at position 1, intermediate at positions 3 and 5, peaked at position 7 and declined thereafter. The pattern for eggs and crawlers per adult was similar to the pattern for eggs and crawlers per gall.

We observed other arthropods within galls. On day 177, 7 thrips or mites of undetermined species were seen out of 65 galls. On day 215, there were 8 such arthropods for 697 galls. On day 252, 17 were seen out of 402 galls, and on day 286 three were seen out of 610 galls.

Cane length reduction was explained by cumulative phylloxera population. The regression equation was $y = -107 \ln (x) + 3666$ ($R^2 = 0.72$; $p = 0.016$).
There was a 21 % decrease in cane length with a cumulative phylloxera population of 10,000 gallicoles per cane.

Gallicoles on different cultivars: Leaf positions had statistically indistinguishable numbers of galls per leaf (Tab. 3). On the other hand, total gallicoles (including eggs) per leaf differed by position: position 5 from the shoot terminal had the highest number of gallicoles per leaf and position 1 had the lowest. Phylloxera numbers segregated by life stage showed that immatures were most numerous at positions 1 and 2 while adults and eggs including crawlers peaked at position 5. The pattern for eggs per adult showed a lower number for position 1

Table 3

Gall and gallicole phylloxera population counts (mean ± SD) on grape rootstock leaves by leaf position on the shoot. Counts were made on leaves collected from six rootstock cultivars on day 224 of 1998 (13 August)

Leaf position	Galls per leaf	Total gallicoles per leaf	Immatures per gall	Adults per gall	Eggs[a] per gall	Eggs[a] per adult
1	89 ± 84	315 ± 516 c	1.34 ± 1.01 a	0.15 ± 0.32 b	5 ± 13 c	20 ± 17 b
3	94 ± 74	1,454 ± 1,956 b	0.95 ± 0.56 ab	0.70 ± 1.24 ab	16 ± 21 bc	25 ± 19 ab
5	99 ± 98	5,730 ± 6,351 a	0.54 ± 0.60 bc	1.03 ± 0.57 a	60 ± 53 a	56 ± 30 a
7	65 ± 64	4,766 ± 5,716 ab	0.52 ± 0.82 bc	1.02 ± 0.72 a	49 ± 35 a	49 ± 22 a
9	50 ± 69	2,193 ± 4,710 ab	0.42 ± 0.51 c	1.02 ± 0.84 a	37 ± 36 ab	36 ± 19 ab
ANOVA*	F = 1.402 P = 0.239	F = 5.228 P = 0.001	F = 4.902 P = 0.001	F = 4.112 P = 0.004	F = 7.887 P = 0.000	F = 5.680 P = 0.001

[a] Tally for eggs includes crawlers (see text for explanation).
* The ANOVA had df = 4 for each of the dependent variables in the table with F and P values as shown.
Values in columns associated with different letters are statistically different from one another at $\alpha = 0.05$ by an LSD test.

than thereafter. The average number of immature- plus adult phylloxera was <2 per gall (Tab 4). The number of feeders per gall on the cultivar T. K. 5 BB, ranged to 7 adults and 4 immatures. The gall maximum on 101-14 MGT was 7 adults and 5 immatures. On Fercal the maximum was 8 adults and 5 immatures.

The highest counts of galls and total gallicoles per leaf were on cultivars Fercal, 101-14 MGT, T. K. 5 BB, and Teleki 5 C and with lower numbers on Rupestris du Lot and *V. amurensis* (Tab. 4). For all cultivars gallicoles per leaf (dependent variable) regressed against galls per leaf (independent variable) was described by the equation
$y = 36.9 - 120.1$ with $R^2 = 0.848$.
Neither measure of fecundity differed statistically by cultivar.

Discussion

Developing galls often contained multiple immatures suggesting that founders in close proximity on an expanding leaf can share in the induction of a single gall. Presence of higher numbers of feeders in mature galls than observed in developing galls, suggests that offspring of the original gall-inducing insects sometimes remained to feed within the parental gall, to begin a second generation. Alternatively, crawlers leaving their home gall might enter other galls. In either case the number of feeding phylloxera exceeds the number of galls. However, the regression of gallicoles against galls per leaf suggests that for sampling purposes, galls per leaf is a reasonable predictor of gallicole population. The increase in adults and egg counts with leaf position was evident in both the Teleki 5 C seasonal study and the cultivar study. Both adult and egg counts reached their peak by position 5 or 7 (Tabs. 2 and 3). This suggests that for purposes of estimating gallicole populations, routinely sampling leaf positions 5-7 from the growing terminal will give consistent results. Instances of high numbers of adults in a single gall suggest that a gall may remain supportive of phylloxera feeding long enough for this second generation to produce offspring of its own. Even with high numbers of phylloxera per gall, galls senesce over time as suggested by decreasing fecundity by leaf positions 11 and 13 (Tab. 2).

The number of eggs per adult was highest at the beginning of the season (day 177) with a steady numerical and statistically real decline as the season progressed (Tab. 1). Carey (1983) suggests that fecundity may be a function of nutrients available to a reproducing insect; therefore, this trend suggests that galls are more nutritious for phylloxera early in the growing season and become less nutritious as the season progresses. By the end of the season fecundity was only a third of what it was in June suggesting a substantial degradation of nutrients galls were able to provide. This drop in reproductive potential is mirrored by the demographic patterns of root-living phylloxera: the highest percentage of the population in the egg stage occurred in spring and the nadir was reached at harvest (Omer *et al.* 1997). An alternative explanation is that the insects' intrinsic reproductive ability drops as the number of generations since the beginning of the growing season increases (Stevenson 1975). This explanation is not supported by the drop in fecundity of insects of almost equal age and generation observed in the leaf position data (eggs per adult, leaf position 9 *vs.* 13, Tab. 2). If intrinsic reproductive ability were involved, we would not expect this drop in fecundity with such a small change in leaf position.

Only few representatives of other arthropod groups were observed in galls, and those observed were not necessarily predators. This situation is in marked contrast to the native range where natural enemies in galls abound (Stevenson 1967).

Production of crawlers by gallicoles is important to the distribution of this insect because of their common

Table 4

Gall and gallicole phylloxera population counts (mean ± SD) on grape rootstock leaves by cultivar using the data considered over all leaf positions. Counts were made on leaves collected from five rootstock cultivars on day 224 of 1998 (13 August)

Cultivar	Galls per leaf	Gallicoles per leaf	Immatures per gall	Adults per gall	Eggs[a] per gall	Eggs[a] per adult
Fercal	116 ± 100 a	3,194 ± 5,243 a	0.63 ± 0.60	0.54 ± 0.52 abc	23 ± 30	34 ± 21
101-14 MGT	110 ± 94 a	3,662 ± 3,728 a	1.14 ± 1.23	1.21 ± 1.29 a	46 ± 43	41 ± 30
T.K. 5 BB	99 ± 55 a	4,697 ± 6,511 a	0.89 ± 0.66	0.98 ± 0.77 ab	43 ± 49	38 ± 24
Teleki 5 C	64 ± 46 a	2,731 ± 5,020 a	0.52 ± 0.45	0.58 ± 0.50 bc	30 ± 38	43 ± 30
Rupestris du Lot	10 ± 20 b	173 ± 446 b	0.40 ± 0.45	0.34 ± 0.37 c	16 ± 17	45 ± 17
V. amurensis[b]	15 ± 7	76 ± 99	0.19 ± 0.35	0.16 ± 0.13	3 ± 3	45 ± 17
ANOVA*	F = 7.903 P = 0.000	F = 2.602 P = 0.041	F = 2.473 P = 0.051	F = 3.084 P = 0.020	F = 1.574 P = 0.189	F = 0.288 P = 0.885

[a] Tally for eggs includes crawlers (see text for explanation).

[b] Because the *V. amurensis* data were collected from only one shoot (see text for explanation), they were not included in analysis.

* The ANOVA had df = 4 for each of the dependent variables in the table with F and P values as shown.

Values in columns associated with different letters are statistically different from one another at $\alpha = 0.05$ by an LSD test.

wind distribution (HAWTHORNE and DENNEHY 1991; DOWNIE 1999, 2000). This movement would tend to equalize the arrival of phylloxera on all vines in a vineyard. Phylloxera's patchy distribution is therefore likely due to factors other than arrival of insects.

Differences in susceptibility of grape species and cultivars to gall formation has been noted many times (RILEY 1876, STEVENSON 1970 b, GALET 1982, WAPSHIRE and HELM 1987). Our data corroborate the previous results. However, where other researchers have limited counts to gall number we have taken the next step and evaluated gallicole numbers and fecundity. The statistical analysis does not suggest that gallicole number is a better indicator of a cultivar's proclivity to support phylloxera. However, it is curious, that fecundity (eggs/adult) does not differ with cultivar even on the cultivars, such as Rupestris du Lot, which supports galls poorly (Tab. 4). This suggests that differences in ability to support leaf feeding phylloxera is due to gall formation and/or survival rather than nutritional content of the leaves for phylloxera.

Lastly, we have provided preliminary data demonstrating decreased vine productivity as a result of gallicoles presence. Decreased cane length is of economic importance to commercial rootstock nurseries and therefore measurement of decreased cane length as a function of gallicole number under varying conditions may serve as the basis for an economic threshold for phylloxera control procedures.

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