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Author(s): V. Mazzoni, G. Anfora, C. Ioriatti, and A. Lucchi Source: Annals of the Entomological Society of America, 101(6):1003-1009. Published By: Entomological Society of America DOI: <u>http://dx.doi.org/10.1603/0013-8746-101.6.1003</u> URL: <u>http://www.bioone.org/doi/full/10.1603/0013-8746-101.6.1003</u>

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## Role of Winter Host Plants in Vineyard Colonization and Phenology of Zygina rhamni (Hemiptera: Cicadellidae: Typhlocybinae)

V. MAZZONI,<sup>1,2,3</sup> G. ANFORA,<sup>1</sup> C. IORIATTI,<sup>1</sup> and A. LUCCHI<sup>2</sup>

Ann. Entomol. Soc. Am. 101(6): 1003-1009 (2008)

ABSTRACT Zygina rhamni Ferrari (Hemiptera: Cicadellidae: Typhlocybinae) is a mesophyll-feeding leafhopper that infests grapevine, Vitis vinifera L. This leafhopper's overwintering strategy and the dynamics of its vineyard colonization, relative to the distance between the grapevines and the winter host plants and different grapevine vegetative densities, are described herein. This species shows a facultative heteroecious life cycle. In autumn, it migrates from vineyards to bramble, *Rubus* gr. *fruticosus*, and rose, *Rosa chinensis* Jacquin. On these host plants, females lay eggs that start to hatch at the end of March. Adults that developed on bramble colonize grapevines beginning in May; the leaf fall of rose, which takes place during the first half of April, probably causes the death of unhatched eggs and nymphs. We found that overwintering females can move back to vineyards and lay eggs until early June. The dynamics of vineyard colonization by the leafhopper involved initial concentration in areas close to bramble (May–early July) with subsequent, progressive spread through the vineyards, with concentration in areas of high vegetative density. Leafhopper presence was negligible in areas of vineyards with levels of vegetative density below a certain threshold.

KEY WORDS leafhoppers, overwintering strategy, Rubus gr. fruticosus, Vitis vinifera, Rosa chinensis

The leafhopper Zygina rhamni Ferrari (Hemiptera: Cicadellidae: Typhlocybinae) is found in southern Europe (Hoch 2007). During the summer, it is monophagous on grapevine, Vitis vinifera L. It feeds mainly on leaf mesophyll cells and causes a progressive reduction in the amount of chlorophyll at the leaf surface and eventual phylloptosis (Vidano 1958). To date, no studies have been undertaken to examine this insect's potential for causing economic damage to vine production, even though other leafhoppers of the same tribe, Erythroneurini, that have the same feeding pattern are economically important pests on grapevine in California (Settle and Wilson 1990), the eastern Mediterranean region (Yigit and Erklc 1992), and the Middle East (Latifian et al. 2005). The harm caused by this insect depends primarily on whether it forms abundant colonies on grapevine leaves. In recent years, severe infestations have been reported in several vine-growing areas in central and southern Italy (Viggiani et al. 2003a, Mazzoni et al. 2004). Because Z. *rhamni* is rather thermophilic, this phenomenon is consistent with the progressive climatic warming that has been noticed in the Mediterranean region (Giorgi and Lionello 2008).

An early study (Vidano 1958) reported that Z. *rhamni* has two to three generations during the summer before adults move, in October, to the wintering hosts, particularly bramble (*Rubus* spp.). All males die within April so that only females are able to reimmigrate back to the vineyards in May. More recent investigations have revealed the presence of *Z. rhamni* eggs and nymphs in the spring on bramble (Pavan 2000, Viggiani et al. 2003b, Mazzoni 2005) and ornamental roses (*Rosa* spp.) (Mazzoni 2005). The latter are often planted near vineyards for early detection of powdery mildew outbreaks, *Erysiphe necator* Schwein. However, the role of bramble in the overwintering strategy of *Z. rhamni* has not been clarified; thus, previous statements regarding a heteroecious life cycle—seasonal alternation of host plants—could not be supported.

In this research project, we focused on the overwintering strategy of *Z. rhamni*, with the aim of clarifying the roles of bramble and rose as oviposition sites. Furthermore, we investigated whether the observed heteroecy is obligatory or facultative and how the presence of bramble hedges in proximity to vineyards may affect the dynamics of leafhopper infestation. This information is essential to determine the potential economic importance of this species.

### Materials and Methods

Study Sites. The research was carried out from August 2005 to October 2006 at Riparbella (Pisa, Italy, 43° 21'4" N, 10° 36'2"E; 180 m above sea level [a.s.l.]) and Matraia (Lucca, Italy, 43° 54'N, 10° 34"E; 150 m a.s.l.) in two vine-growing areas of western Tuscany (central

<sup>&</sup>lt;sup>1</sup> Plant Protection Department, IASMA Research Centre, via E. Mach 1, 38010 San Michele all'Adige (TN), Italy.

<sup>&</sup>lt;sup>2</sup> Dipartimento Coltivazione e Difesa Specie Legnose "G. Scaramuzzi", Sezione Entomologia Agraria, University of Pisa, via S. Michele degli Scalzi 2, 56124 Pisa, Italy.

<sup>&</sup>lt;sup>3</sup> Corresponding author, e-mail: valerio.mazzoni@iasma.it.

Italy). Two moderately sloping vineyards planted with 'Sangiovese' and their surroundings were monitored. At the first site, 5-yr-old plants covered a surface of  $\approx$ 4,600 m<sup>2</sup> with a planting density of 9,050 plants per ha (30 rows spacing of 1.3 m). Bramble hedges (Rubus gr. fruticosus L.) bordered the western side of this vineyard. The eastern side was close to oak trees, myrtle, and mastic trees (Quercus suber L., Quercus ilex L., Myrtus communis L. and Pistacia lentiscus L.), and the southern and northern edges bordered other vineyards. At the second site, 8-yr-old plants covered a surface of  $\approx$ 7,000 m<sup>2</sup> at a density of 4,000 plants per ha (30 rows spacing of 2.5 m). There were bramble hedges along the southeastern border, the southern and the western edges bordered other vineyards, and the northern edge was bordered by myrtle, mastic trees, and some oak (Quercus robur L.), elm (Ulmus minor Miller), and maple (Acer campestre L.) trees. At this site, there was a Chinese rose bush (Rosa chinensis Jacquin) at one end of each row of grapevines. In both vineyards, plants were trained using a spur-pruned cordon system.

**Overwintering Strategy.** The overwintering strategy of *Z. rhamni* was studied from the time of the insects' emigration from grapevine in August, through the following spring. The presence of adults on the grapevines (n = 20) was monitored once every 15 d, from 1 August to 15 October, by sweep-net sampling (three sweeps per plant) in each vineyard. Surveys of leafhopper populations on bramble, rose, and the deciduous bordering plants were conducted once every 15 d from 1 August to 15 October and then once a month through 15 April (20 sweeps per plant species per sampling).

To study the species chromatic variability, at each site, 30 females were randomly chosen and classified by their degrees of pigmentation. These insects were classified as "white" (forma typica) or "red" (f. simplex, f. difficilis and f. manca; Vidano 1958). The same females were then dissected to check for the presence of fully developed eggs in their ovarioles. After the first detection of eggs in ovarioles, six 40-60-cm shoots of bramble and rose were collected once a month near the vineyards to ascertain the beginning of oviposition. The harvested shoots were cut into sections of 10–15 cm each. Each section had 15–20 leaflets. These sections were put into vials filled with water to prevent withering. Groups of five to six shoots were kept together in Plexiglas cylinders (13.5 by 15.0 cm), which were covered at the top with a net and stored in a climate-controlled chamber  $(20 \pm 0.5^{\circ}C, 65 \pm 5\% RH)$ for 15 d. Newly hatched nymphs were daily transferred to bramble cuttings where they were reared to adulthood and then identified by species. The identification keys of Ribaut (1936) and Ossiannilsson (1983) were used to identify the collected insects. This experiment continued until the first detection of Z. rhamni eggs in field.

The first occurrence of *Z. rhamni* nymphs on bramble and rose was checked by direct observation (100 leaflets) every 2 wk beginning 16 January. Because the discernment of *Z. rhamni* from congeneric species is not possible at nymphal stage, all surveyed nymphs were individually reared in the climatic chamber to adulthood on bramble cuttings and then identified.

To ascertain whether the species heteroicy is obligatory or facultative, the longevity and egg-laying ability into grapevine leaves of overwintering females were investigated. At the first appearance of nymphs in the field, an aspirator was used to collect 20 overwintering females from brambles. Females were kept individually in Plexiglas cages on a rooted grapevine leaf. Weekly, until their death, the females were moved into another cage with a new leaf. The leaves, after the removal of the females, were kept under rearing conditions  $(20 \pm 0.5^{\circ}C, 65 \pm 5\% \text{ RH})$  for 30 d to allow any eggs to hatch. Furthermore, because our preliminary observations had showed the exclusive presence of white females in spring on grapevine, we verified a possible gradual red pigment regression in the overwintering females. Each insect was assigned to a pigment category, first at the capture and secondly at the death, according to the description given by Vidano (1958). We defined the total absence of red cuticular pigment (forma *typica*) as Type 0, the presence of weak red stripes on wings (forma difficilis) as Type 1, the presence of red stripes on head and thorax (forma manca) as Type 2, and the presence of red stripes on both the head/thorax and wings (forma simplex) as Type 3.

Migration and Distribution in the Vineyards. To study the distribution of the leafhopper population in the vineyards, 18 yellow sticky traps (25 by 12 cm; Glutor, Intrachem, Bologna, Italy) were positioned in each vineyard and replaced every 10 d from 30 April to 4 October 2006. Each trap was placed 1.5 m above the ground on an iron-wire grapevine stake. The traps were set at different distances (3-120 m; Table 2) from the vineyard border closest to bramble hedges. Because the leafhopper population density could be influenced by different vegetation gradients, an indicator of grapevine vegetative density also was considered. In June, the vegetative density of an area of 50 m<sup>2</sup> around each sticky trap was measured in terms of the number of primary shoots per square meter (Table 2). Differences in the density of vegetation were primarily due to differences in the vigor of the plants.

To characterize the adult population present in the vineyards during the immigrant phase, besides the use of sticky traps we did also three sweep-net samplings (20 May, 19 June, and 15 July). We measured the following parameters: number of captured specimens per trap, percentage of females of the total captures in the traps, percentage of red-pigmented specimens of 30 sweep-net-sampled females, and percentage of 30 sweep-net-sampled females.

To describe the dynamics of the migration of *Z. rhamni* from its winter hosts to grapevine, the first presence of eggs and nymphs in the vineyards also was checked once every 10 d during May and June. Nymphs were searched on five leaves taken from the median-basal part of 20 randomly chosen grapevines. To detect eggs, the same leaves were then kept under

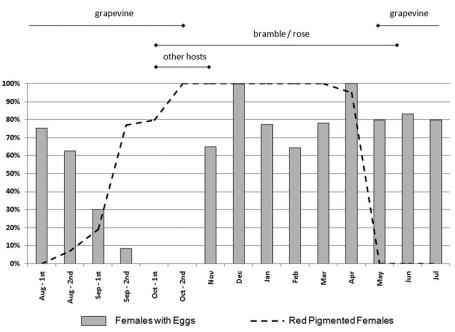


Fig. 1. Proportion (percentage) of Z. *rhamni* females (n = 30) with fully developed eggs in their ovarioles and of red type females over the course of the year. Samplings were performed every 15 d from August to October 2005 and monthly from November 2005 to July 2006. The plant species on which the adult insects were found are reported above the chart.

rearing conditions  $(20 \pm 0.5^{\circ}C, 65 \pm 5\% \text{ RH})$  for 15 d to allow for nymphal emergence.

Statistical Analysis. The insects captured on each trap were analyzed in three distinct phases: immigrant phase (IP; May–15 July), residential phase (RP; 15 July-August), and emigrant phase (EP; September-October). Kendall rank-order correlations between the number of captured insects and the distance from overwintering hosts and between the number of captured insects and grapevine vegetative density were performed. The effect of a confounding variable was tested using Kendall partial rank-order correlations that excluded either distance or density (Siegel and Castellan 1988). The effects of both distance and density were evaluated for both locations. A change point analysis was performed to estimate the beginning of a new trend (change point [CP]) within the series, concerning either distance (only data from IP) or density (IP + RP + EP). The cumulative sum statistic (Cusum) method was used to estimate the CP in sequentially ordered data (Pettitt 1979). The estimation corresponded to the point at which the cumulative difference between the average value and each individual value reached the largest absolute value. To test the null hypothesis that there was no CP, the Wilcoxon-Mann-Whitney test (one-tailed) was used to compare the two data series, before and from the candidate CP (Siegel and Castellan 1988).

#### Results

**Overwintering Strategy.** The phenology of Z. *rhamni* is detailed in Fig. 1. Leafhoppers were collected on grapevine until leaf fall (late October). From the beginning of October, many adults also were collected from shrubs and trees near the vineyards. Noticeable leafhopper populations were observed on elm, oaks (both *Q. robur* and *Q. ilex*), rose and bramble. However, after November, adults of *Z. rhamni* were found exclusively on rose and bramble.

The first appearance of red females was observed in August, whereas, earlier in the season, the white type was the only one captured in the vineyards. From late September most of the females were red. Developed eggs were first found in red females on 15 November (Fig. 1).

On 16 January, Z. *rhamni* and other typhlocybinae eggs were first obtained from bramble and rose tissues. Z. *rhamni* eggs represented 23 and 54% of total detected eggs, respectively, on bramble and rose. Among the other leafhoppers, Zygina schneideri Günthart and three species of the genus *Ribautiana*, R. *cruciata* (Ribaut), R. *debilis* (Douglas), and R. *tenerrima* (Herrich-Schäffer), were rather abundant on bramble, whereas Zygina discolor (Horvath) and Edwardsiana rosae (Edwards) were abundant on rose (Table 1).

Nymphs were first observed in the field on 31 March. All species collected previously as eggs also were collected as nymphs. *Z. rhamni* nymphs constituted 8 and 45% of the bramble and rose leafhopper population, respectively (Table 1).

During this part of the year, we found only red females, most of which were carrying developed eggs. In our experiments, all the overwintering females collected and reared from 31 March, survived until early May. More than 50% (11 females) survived until late

		$Eggs^{a}$				Nymphs <sup>b</sup>			
	Bramble		Rose	Total	Bram	ble	Rose	Total	
	Riparbella	Matraia	Matraia		Riparbella	Matraia	Matraia		
Zygina rhamni	17	48	34	99	6	11	17	34	
Zygina discolor			10	10			9	9	
Zygina schneideri	13	24		37	2	7		9	
Ribautiana cruciata	51	26		77	43	54		97	
Ribautiana debilis	35	21		56	14	17		31	
Ribautiana tenerrima	13	20		33	21	16		37	
Edwardsiana diversa	0	2		2		3	3	6	
Edwardsiana platanicola	13	0		13	4			4	
Edwardsiana rosae			19	19		1	9	10	
Total	142	141	63		90	109	38		

Table 1. Leafhopper eggs and nymphs collected from bramble and rose plants at Riparbella and Matraia

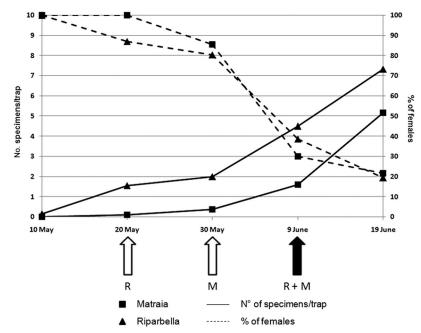
<sup>a</sup> Number of individuals hatched under laboratory conditions (16 January 2006).

 $^b$  Number of nymphs collected in the field (31 March 2006).

May, whereas all were dead by 10 June. All of these females were able to lay eggs on grapevine leaves until their death. A decline in the pigmentation level of the females was observed over time. On 31 March, most of the captured females displayed red phenotypes, particularly Type 2 (Type 0, 1 insect; Type 1, 6 insects; Type 2, 8 insects; and Type 3, 5 insects). However, at their deaths, the majority exhibited the white phenotype (Type 0, 11 insects; Type 1, 7 insects; Type 2, 2 insects; and Type 3, 0 insects).

Migration and Diffusion in Vineyards. The first appearance of *Z. rhamni* adults in the vineyards was noted in early May (10 and 11 May at Riparbella and Matraia, respectively) at which time only a few females were captured. A noticeable increase in the number of captures was recorded at the end of May, corresponding with the first appearance of males. Soon, the proportion of males exceeded that of females. Eggs were first collected from *V. vinifera* on 21 May (Riparbella) and 31 May (Matraia); nymphs were first detected on 11 June (Riparbella) and 10 June (Matraia; Fig. 2).

The captures of each yellow sticky trap set in the vineyards are shown in Table 2; the results of the partial correlation analysis are reported in Table 3. Most of the captured insects were collected from nearby bramble hedges before the end of August (Riparbella. IP:  $\tau_{1, 3/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0.391$ , P < 0.01; RP:  $\tau_{1, 13/2} = -0$ 



**Fig. 2.** Mean number of adult *Z. rhamni* (unbroken line) and percentage of females (broken line) captured on yellow sticky traps during the colonization phase of the infestation cycle (May and June 2006). Data from Riparbella are represented by lines with triangles and data from Matraia by lines with squares. Empty arrows indicate the first detections of eggs in grapevine leaves in Riparbella (R) and Matraia (M). The black arrow indicates the date on which the first nymphs were detected in the field.

Table 2. Number of Z. rhamni adults captured on each sticky trap between May and October 2006 at Riparbella and Matraia"

Riparbella			Captures				Matraia			Captures			
Trap	Distance (m)	Density (s/m <sup>2</sup> )	IP	RP	EP	Total	Trap	Distance (m)	Density (s/m <sup>2</sup> )	IP	RP	EP	Total
1	3	5.1	71	200	89	360	1	5	5.4	77	136	26	239
2	6	5.0	117	327	51	495	2	7.5	4.0	18	43	8	69
3	15	6.3	50	128	158	336	3	12.5	5.2	78	460	226	764
4	27	3.6	6	46	21	73	4	20	5.2	80	478	226	784
5	30	5.3	20	103	49	172	5	20	6.1	76	287	100	463
6	30	5.7	39	144	106	289	6	25	1.9	12	40	8	60
7	50	5.1	22	89	88	199	7	32.5	5.3	54	326	208	588
8	50	6.3	51	205	284	540	8	35	2.0	9	61	9	79
9	51	3.5	2	38	27	67	9	40	4.3	9	54	13	76
10	65	3.4	18	68	58	144	10	40	4.8	49	220	78	347
11	65	5.9	17	96	91	204	11	50	5.6	53	279	141	473
12	66	2.3	5	17	14	36	12	52.5	4.9	44	148	32	224
13	85	5.2	29	204	236	469	13	60	5.6	21	83	17	121
14	90	2.4	5	18	14	37	14	60	5.6	54	260	100	414
15	90	4.2	19	57	49	125	15	70	3.6	3	29	8	40
16	110	2.4	3	12	5	20	16	90	5.7	37	170	92	299
17	115	1.1	5	20	8	33	17	90	6.1	45	220	68	333
18	116	2.0	3	16	2	21	18	120	3.8	11	41	8	60

<sup>*a*</sup> Data reported in the columns are the distance of the trap (meters) from the closest bramble bush; the mean vegetative density (shoots per square meter) in 50 m<sup>2</sup> of vineyard around the trap; the accumulated captures for each phase of the season (IP, immigrant phase; RP, residential phase; EP, emigrant phase); and the total numbers of captured insects.

 $\begin{array}{l} -0.355,\,P<0.025;\,\text{EP:}\,\tau_{1,\;13/2}=-0.101,\,P>0.25;\,\text{and}\\ \text{Matraia. IP:}\,\tau_{1,\;3/2}=-0.452,\,P<0.005;\,\text{RP:}\,\tau_{1,\;3/2}=\\ -0.298,\,P<0.05;\,\text{EP:}\,\tau_{1,\;3/2}=-0.241,\,P>0.05).\\ \text{However, the numbers of captured insects were significantly correlated with grapevine vegetation density throughout the survey period (Riparbella. IP:\\ \tau_{2,\;3/1}=0.393,\,P<0.025;\,\text{RP:}\,\tau_{2,\;3/1}=0.494,\,P<0.005;\\ \text{EP:}\,\tau_{2,\;3/1}=0.705,\,P<0.001;\,\text{and Matraia. IP:}\,\tau_{2,\;3/1}=0.507,\,P<0.005;\,\text{RP:}\,\tau_{2,\;3/1}=0.525,\,P<0.001;\,\text{EP:}\,\tau_{2,\;3/1}=0.515,\,P<0.001).\\ \end{array}$ 

The CP analysis allowed the definition of capture thresholds according to vegetative density (the entire season) and distance (immigrant phase) gradients (Table 3). In both the vineyards, the *Z. rhamni* population was constantly concentrated in areas characterized by vegetative density above a similar value (Riparbella: CP = 4.2 shoots per m<sup>2</sup>,  $T_w = 37$ , P < 0.001; and Matraia: CP = 4.3 shoots per m<sup>2</sup>,  $T_w = 21$ , P < 0.001). Conversely, the distance CP was rather different between the sites, although it showed a clear

population aggregation in vineyard areas closest to the bramble hedges during the immigrant phase (Riparbella: CP = 50 m,  $T_w = 110$ , P < 0.005; and Matraia: distance CP = 20 m,  $T_w = 98$ , P < 0.01.).

#### Discussion

The current study stresses the importance of bramble in the *Z. rhamni* life cycle. Bramble is the main host plant for overwintering adults and the following spring generation, and it also represents the major external source of insects for colonizing vineyards. Although recent studies (Pavan 2000, Viggiani et al. 2003b) addressed the ability of the species to develop an additional generation on bramble in the spring, they did not fully clarify some aspects of the life cycle of the leafhopper and the influence of the winter hosts on the colonization of nearby vineyards.

Our study also demonstrated the potential for overwintering females to return to grapevine in late spring.

Table 3. Statistical analyses of the diffusion of Z. rhamni in the vineyards at Riparbella and Matraia

	Sites		Partial correlation analysis <sup>a</sup>											
Variable		IP		RP		EP		Change point analysis <sup>b</sup>						
		τ	Р	$\tau$	Р	$\tau$	Р	Т	m	Р	СР			
Distance	Riparbella $\tau_{1,3/2}$	-0.391	< 0.01	-0.355	< 0.025	-0.101	>0.25	110	8	< 0.005	50 m			
Density	Matraia $ au_{1,3/2}$ Riparbella $ au_{2,3/1}$ Matraia $ au_{2,3/1}$	-0.452 0.393 0.507	$< 0.005 \\ < 0.025 \\ < 0.005$	-0.298 0.494 0.525	$<\!$	-0.241 0.705 0.515	> 0.05 < 0.001 < 0.001	98 37 21	5 8 6	$<\!$	20 m 4.2 sh/m <sup>2</sup> 4.3 sh/m <sup>2</sup>			

<sup>*a*</sup> Results of the Kendall rank-order partial correlation analysis. The correlations between distance from bramble and the number of captured adults and between grapevine vegetation density and the number of captured adults are reported for each site. The Kendall  $\tau$  value and respective probability for each seasonal phase,  $\tau_{1, 3/2}$  with the exclusion of the density factor and  $\tau_{2, 3/1}$  with the exclusion of the distance factor, are listed in the columns.

are listed in the columns. <sup>b</sup> Results of the change point analysis. For each factor and site, the value of T (Wilcoxon–Mann–Whitney test, one-tailed), the number of traps (m) assigned to the series of data before the change point, and the probability (P) and estimated value of the change point (CP) are listed. The analysis of the distance effect was performed using data pertaining to the immigrant phase (IP); the analysis of the density effect also included the residential phase (RP) and the emigrant phase (EP) data. Although females of *Z. rhamni* females began to lay their eggs in January on winter hosts, they could oviposit on grapevine in May–June, at the end of their lives. In our experiments, overwintering females could survive until June for a total life span of 9–10 mo, which is much longer than the life spans of females of the spring and summer generations. Consequently, *Z. rhamni* may be considered to be a facultative heteroecious species (between bramble/rose and grapevine), in that overwintering females can lay eggs on both the winter and the summer hosts. Facultative alternation among different hosts during the year is not rare in leafhoppers and also has been described for other mesophyll-feeding typhlocybinae (Claridge and Wilson 1978).

However, the absence of red females in the vineyards in spring does not contrast this view. In fact, the distinction between winter and spring females is not possible on the basis of color features because the red pigment is progressively lost from April to the point that finally the appearance of individuals of the two generations is identical. This reduction in pigment is probably caused by increasing temperatures, as has been shown for Zygina suavis Rey under laboratory conditions (Vidano 1961). Conversely, red-colored specimens were first detected in vineyards during the second half of August as temperatures were dropping, and in September most of the population of Z. rhamni was fully colored. It is likely that decreasing temperatures also can induce a reproductive diapause in females, because we did not find any eggs in red specimens before November. During this diapause, many individuals move to different intermediate hosts (e.g., elm, oak). At the end of November, the first detection of eggs in overwintering females coincided with a further population shift toward the winter hosts bramble and rose.

In spring, Z. rhamni offsprings constituted a remarkable part of the entire leafhopper population on bramble that, consequently, represents an important factor in the species life cycle in the studied environments. In late May, the first appearance of males indicated both the colonization of vineyards by insects hatched from eggs laid in bramble and the first emergence of offspring from eggs laid in grapevine leaves by overwintering females. However, our surveys during the first half of May involved the capture of a very small number of females and did not reveal the presence of nymphs or eggs on V. vinifera. This suggests that overwintering females play a minor role in determining the first Z. rhamni peak of flight as detected by yellow sticky traps in the vineyards in early June. It is more likely that these two sources of vineyard infestation overwintering females and the new spring generation-may vary in importance in different climates and biotopes. Furthermore, the variable occurrence of egg parasitoids, such as fairyflies (Hymenoptera: Mymaridae) can affect the hatching rate and subsequent vineyard colonization (Viggiani et al. 2003b, Ponti et al. 2005).

Z. *rhamni* eggs and nymphs were also abundant on rose plants located near the vineyards. However, the

role of ornamental roses as oviposition sites and nymphal host plants requires further clarification. In fact, despite the high number of nymphs that we collected from rose at the end of March, this population was probably almost completely erased by the leaf fall that started in winter and ended around the middle of April. This phenomenon highlights the potential of R. chinensis for use as a trap-plant for Z. rhamni. By planting rose bushes near the vineyards, it would be possible to abate part of the spring population, especially in those situations in which there are no nearby bramble plants. This could be a new application of the "push and pull" strategy (Cook et al. 2007), with the plants used not only attracting the insect pest during its migration but also inducing high mortality by preventing full development of the subsequent generation.

The oviposition of overwintering females in bramble can be considered an important factor in predicting the pattern of vineyard infestation. It is noteworthy that during the first part of the summer, through the middle of July, most of the *Z. rhamni* population was concentrated in those areas of the vineyard adjacent to bramble hedges. The inverse correlation between distance from brambles and the number of insects captured on sticky traps indicates bramble as the main source of the infestation and also indicates that the establishment of the pest population throughout the vineyard is a slow progressive process.

We also found that, during the season, areas of the vineyards that had less than a certain threshold level (4.2–4.3 shoots per m<sup>2</sup>) of vegetative density were almost deserted by the species. Consequently, the leafhopper distribution in the vineyard resulted in aggregations, according to vegetative density gradients. An aggregated distribution also has been reported for other grapevine leafhoppers—adult and nymphal *Empoasca vitis* Goethe (Bosco et al. 1997, Maixner 2003) and *Jacobiasca lybica* Bergevin & Zanon (Delrio et al. 2001) and nymphal *Scaphoideus titanus* Ball (Lessio and Alma 2006), but it has not been correlated previously to the presence or absence of alternative or overwintering hosts.

When a species requires different host plants at different times during the life cycle, such resources play a complementary role in the landscape for the insect biology. As a consequence, if the complementary plants are adjacent in a certain environment, then it can be a favorable habitat for a particular species (Dunning et al. 1992). For Z. rhamni, the presence of bramble in proximity to vineyards would support a larger population than in those situations where the two plants are far apart. However, the importance of the bramble as a source of biodiversity and as a habitat for antagonists also must be carefully considered. The knowledge of the landscape structure and insect phenology can be useful for the development of pest management strategies, by rationalizing sampling plans or treatments and defining economic thresholds.

November 2008

We thank V. Trivellone for valuable collaboration in field samplings and L. Soliani (University of Parma) for statistical advice. This research was partially funded by University of Pisa (Fondi di Ateneo 2005) and by the Autonomous Province of Trento (SafeCrop and HOST projects).

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Received 14 April 2008; accepted 11 July 2008.