

Spatial and temporal distribution of *Empoasca vitis* within a vineyard

Damien Decante and Maarten van Helden

UMR Santé Végétale 1065, INRA/ENITA de Bordeaux, 1, Cours du Général de Gaulle 33175, Gradignan Cedex, Bordeaux, France

- Abstract**
- 1 The intra-plot spatial distribution of the green leafhopper *Empoasca vitis* (Goethe) (Cicadellidae, Empoascini) was assessed over three successive growing seasons in a Bordeaux vineyard. Weekly measurements of adult trappings and nymphal counts were performed in a 1.7-ha plot on 130 sampling points.
 - 2 Statistical and geostatistical analyses revealed inconsistent spatial distributions of adults and nymphs in spring, but consistent spatial distributions in summer, which were identical every year.
 - 3 Similarities between spatial distributions of the mobile adults and the sedentary and aggregated nymphs strongly suggest that adults disperse inside the plot to areas preferred for egg deposition.
 - 4 The similarity of summer populations among years suggests that this insects distribution is based on (perennial) differences in plot characteristics.

Keywords Aggregation, cartography, cicadellidae, geostatistics, migration, viticulture.

Introduction

Insects such as leafhoppers and planthoppers (Hemiptera – Auchenorrhyncha) show frequent migrations (DeLong, 1971; Taylor, 1985; Della Giustina, 2002) that influence their population dynamics and spatial distributions. These migrations have to be taken into account for adequate Integrated Pest Management strategies (Lamp & Zhao, 1993; Holt *et al.*, 1996; Ishii-Eitman *et al.*, 1997; Irwin, 1999; Jeger, 1999; Matsumura & Suzuki, 2003; Orenstein *et al.*, 2003; Emmen *et al.*, 2004; Decante & van Helden, 2006).

Adults of the polyphagous green leafhopper *Empoasca vitis* (Goethe), a European vine pest, overwinter outside the vineyards on evergreen trees and shrubs: the overwintering host plants. Before spring immigration into (and after autumn emigration out of) vine plots, adults can be observed on a wide range of deciduous plants present in the vineyard vicinity: the intermediate host plants (Cerutti *et al.*, 1991; van Helden *et al.*, 2003). Two to four sexual generations develop in vineyards (Cerutti *et al.*, 1991; Bosco *et al.*, 1996; Genini, 2000; Boell & Hermann, 2004), and recurrent inter-plot summer migrations are assumed (Decante & van Helden, 2003, 2006). Adults and nymphs feed on phloem sap, and punctures provoke leaf necrosis (hopperburn: Backus *et al.*, 2005) that result in delayed maturity and reduced sugar content (Vidano *et al.*,

1987; Candolfi *et al.*, 1993; Delbac *et al.*, 1996). Insecticide intervention on nymph populations is sometimes required for summer generations, and intervention thresholds vary from 0.5 to 4–5 nymphs per leaf according to authors and regions (Corino *et al.*, 1992; Baillod *et al.*, 1993; Candolfi *et al.*, 1993; Rousseau, 1994; Delbac *et al.*, 1996).

Most of the studies on *E. vitis* plot populations focus on the influence of the surrounding vegetation (hedges, woodlands and grasslands) as a source of natural enemies, mainly egg parasitoids (Cerutti *et al.*, 1991; Baur *et al.*, 1998; Genini, 2000; van Helden *et al.*, 2003; Boell & Hermann, 2004), but also as alternative host plants for the polyphagous *E. vitis* (Cerutti *et al.*, 1991; Bosco *et al.*, 1996). Finally, the surrounding vegetation may also generate edge effects through microclimatic modifications, shading effects, competition for water and nutrients, air flows, etc. (Baudry *et al.*, 2000; Marshall & Moonen, 2002), which all have an effect on vine-plant characteristics. However, the influence of vine-plant characteristics on *E. vitis* spatial distribution is not taken into account.

At plot scale, population levels of successive generations show large fluctuations that can be attributed to summer migrations (Decante & van Helden, 2003), but inter-plot redistribution of migrating adults and of their offspring have not been connected to plot characteristics (varieties, age, surrounding vegetation; Decante & van Helden, 2006). Within plots, *E. vitis* aggregations are observed (Decante & van Helden, 2006). Moreover, growers indicate that hopperburn

Correspondence: Maarten van Helden. Tel: +33 5 57 35 07 62; fax: +33 5 57 35 07 59; e-mail: m-vanhelden@enitab.fr

symptoms are located in the same area of the plot every year. *Empoasca vitis* and hopperburn spatial distribution could therefore be related to intra-plot spatial variability in biotic and abiotic factors (soil composition, topography, hydrology, etc.) and vine plant characteristics that show similar patterns every year (Bramley & Hamilton, 2004; Bramley, 2005; Taylor, 2005).

In the present study, we report an assessment of spatio-temporal distribution of *E. vitis* at the intra-plot scale over three growing seasons, with a view to determine the appropriate spatial (size and density of monitoring network) and temporal (frequency of observations) scale for monitoring this insect. Type and constancy (within and between years) of intra-plot spatial distribution of successive *E. vitis* stages and generations were examined and the possible effects of intra-plot characteristics and surrounding vegetation considered.

Materials and methods

Vineyard

The study focused on a 1.7-ha vine plot, planted with *Vitis vinifera* cv. Merlot at 5500 plants/ha (1.5 m between rows $\times$ 1.2 m between plants). The plot is located in the 'Cotes-de-Castillon' area, near Bordeaux, France (44°53'01"N, 0°03'47"W). It lies on a nearly flat plateau, has a permanent natural ground cover and is surrounded by other vine plots, except at its western edge, where a slope supports spontaneous mixed woodlands (Fig. 1). It is dedicated to wine production, is managed according to integrated farming standards and has received no insecticide subsequent to 1995.

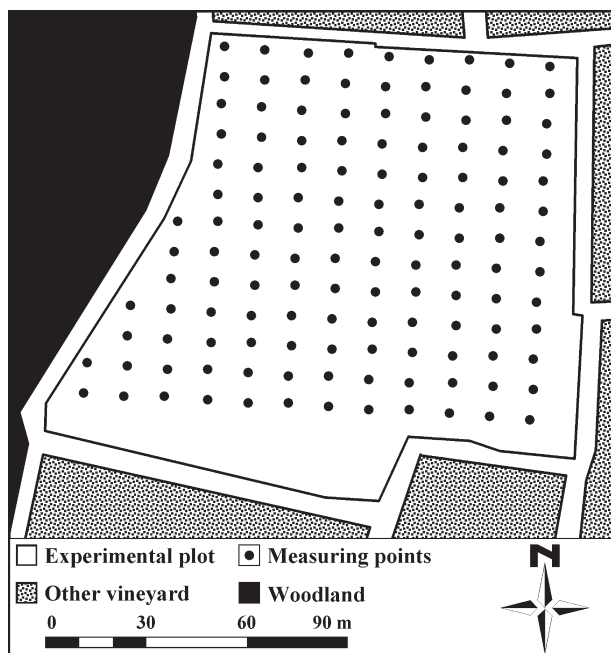


Figure 1 Map of the experimental plot, traps and surrounding vegetation (woodlands and vineyards) of the studied plots.

Data collection

Adult trappings and nymphal counts were performed weekly during three successive growing seasons, from May 1998 to November 2000. One hundred and thirty sampling points were disposed on a regular 9 $\times$ 12 m sampling grid (six rows $\times$ ten plants) (Fig. 1). Adults were sampled with one Yellow Sticky Trap (YST) of 5 $\times$ 15 cm (Biosystemes, France) per point, fixed on the trellis wire under the vine canopy and changed weekly. Nymphs were counted weekly in the vine canopy above the YST on 20 mature leaves (Vidano *et al.*, 1987; Fos *et al.*, 1997) distributed on five consecutive vine plants of the same row.

Data analysis

Empoasca vitis abundance is expressed here as the number of adults caught per YST per week and numbers of nymphs per 100 leaves. Spatial distribution of one weekly adult trapping or nymphal count, measured over the 130 sampling points, is referred to throughout as 'SpD'. Each stage and generation is referred to as the year number (98-99-00), followed by 'A' for adult or 'N' for nymph, with 'x' being the generation number, starting by overwintering/immigrating adults as generation 0. Because it was impossible to distinguish generation A1 from A2, they were considered together as A1-2.

Aggregation levels (I_a) of weekly SpDs

The spatial index of aggregation (I_a) and its associated probability (P) were calculated for each SpD, using the Spatial Analysis by Distance Indices method for spatial clustering (SADIE) (Perry *et al.*, 1999). This method classifies SpD as aggregated ($I_a \gg 1$ and $P < 0.05$), random (no clustering, $I_a \approx 1$ and $0.05 < P < 0.95$) or regular type ($I_a < 1$ and $P > 0.95$), using a randomization test. The contribution of each sampling point toward overall clustering (v) was also calculated.

Temporal consistency (X) of weekly SpDs

The index of association, (X), between consecutive SpDs and its associated probability (P) were calculated using the SADIE method for spatial association. This method measures the overall association X between pairs of (A)SpDs (Perry & Dixon, 2002) with specific features: (i) association value X (i.e. correlation coefficients between sampling point clustering indices ' v ' of the two sets) accounts for the spatial pattern, assessed in the calculation of clustering indices; (ii) probability P for a significant association or dissociation, measured through a randomization test, allows comparison of data sets with any frequency distribution; and (iii) bias in probability P for significant association (or dissociation), generated by spatial autocorrelation over neighbouring sampling points, is accounted for using the method of Dutilleul (1993), which corrects the degree of freedom according to the level of spatial autocorrelation. Couples of consecutive SpDs are classified among 'associated' ($X \gg 0$ and $P < 0.05$); 'independent' ($X \approx 0$ and $0.05 < P < 0.95$) or 'dissociated' ($X < 0$ and $P > 0.95$).

Table 1 Average spatial distribution (ASpD) periods (ISO week numbers), with index of aggregation I_a (in parentheses) for all generations and all years

ASpD	A0	N1	A1–2	N2
1998	19–22 (1.1)	21–25 (1.4)*	24–35 (1.2)	27–32 (3.5)*
1999	17–20 (2.4)*	19–23 (1.0)	25–36 (1.1)	26–31 (2.7)*
2000	16–19 (1.1)	20–24 (1.1)	25–36 (1.2)	28–33 (3.1)*

*Significant aggregation ($I_a > 1$; $P < 0.05$).

Average spatial distribution of stages and generations (ASpDs)

ASpDs (i.e. average trap catches or counts at each sampling point over several weeks) were calculated over population peaks of each stage/generation, with an identical duration

each year. These averaged periods were determined to ensure the inclusion of the highest indices of association (X) within aggregated periods (I_a) of each population peak (Table 1; Figs 2, 3). The ASpD of each *E. vitis* stage/generation was then assessed (I_a value) and compared over the 3 years (X value). ASpDs are referred to throughout the text with the abbreviations of the corresponding stage, generation and year, as explained above.

Variograms and cartography

The spatial structure of each ASpD was monitored with experimental omnidirectional variograms. Semivariances were represented up to distances of 75 m with an increment of 15 m and modelled. The resulting model was used to map the spatial distribution of each ASpD using the Kriging method (Goovaerts, 1999).

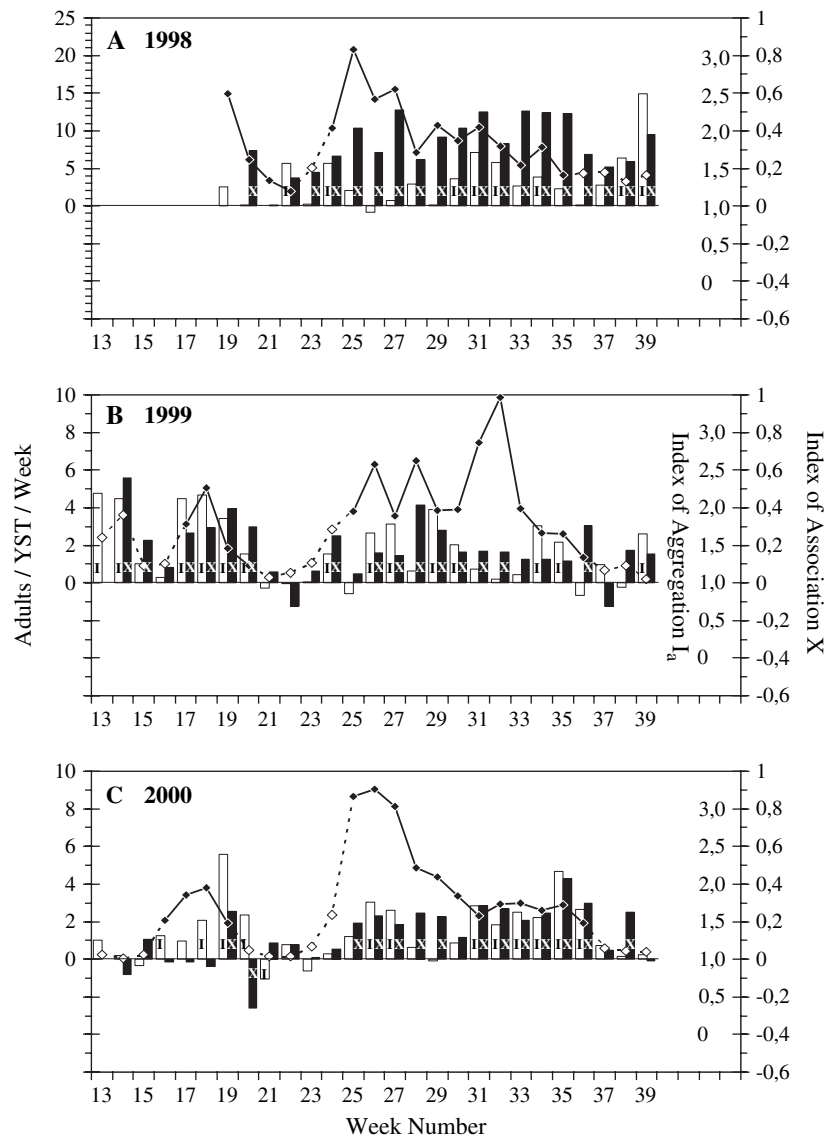


Figure 2 Adult dynamics (line), spatial aggregation I_a (open bars) and spatial association between subsequent weeks X (solid bars) for all 3 years of observation. Trappings included in the average spatial distribution (ASpD) of stages and generations (solid line, ♦) are differentiated from the others (dashed line, ◇). Significant aggregation ($I_a > 1$, $P < 0.05$) or regularity ($I_a < 1$, $P > 0.95$) of each SpD is indicated by I . For each SpD, significant association ($X > 0$, $P < 0.05$) or dissociation ($X < 0$, $P > 0.95$) with the SpD of the preceding week is indicated by X .

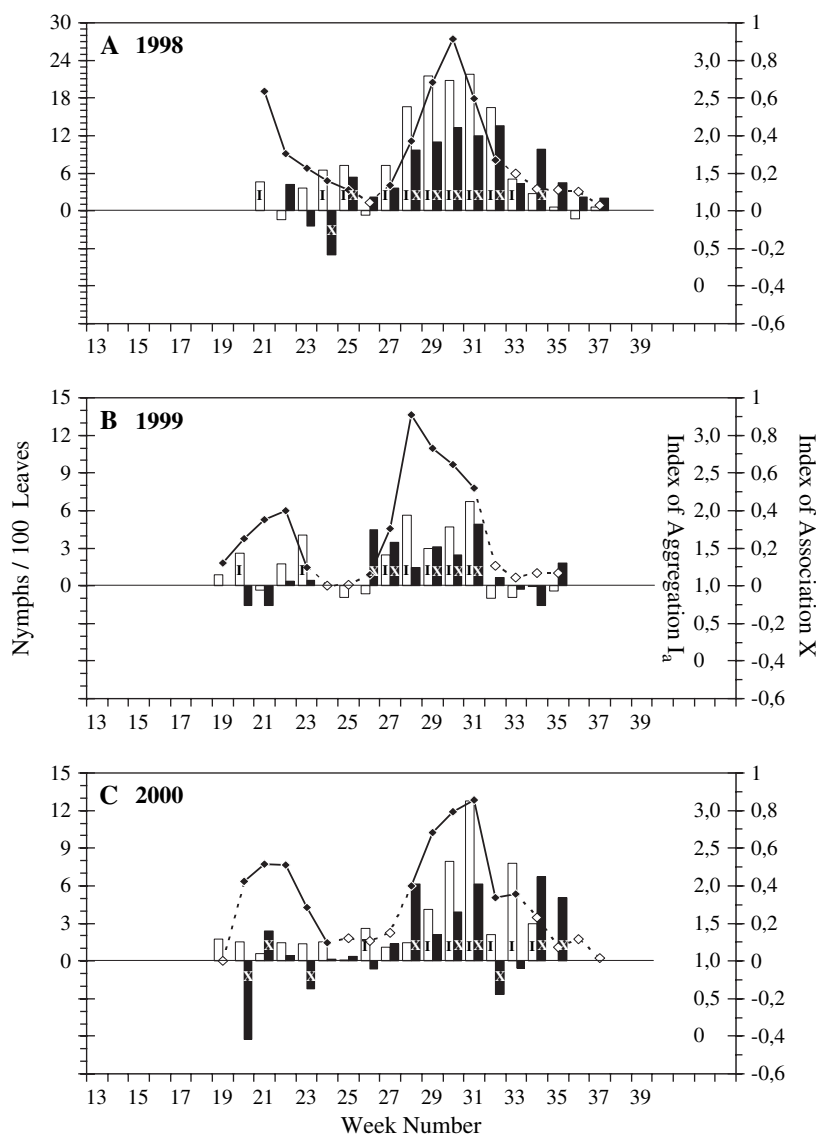


Figure 3 Nymphal dynamics (line), spatial aggregation I_a (open bars) and spatial association between subsequent weeks X (solid bars) for all 3 years of observation. Counts included in the average spatial distribution (ASpD) (solid line, $\blacklozenge$) are differentiated from the others (dashed line, $\diamond$). Significant aggregation ($I_a > 1$, $P < 0.05$) or regularity ($I_a < 1$, $P > 0.95$) of each SpD is indicated by I . For each SpD, significant association ($X > 0$, $P < 0.05$) or dissociation ($X < 0$, $P > 0.95$) with SpD of the preceding week is indicated by X .

Results

Population dynamics

Adult and nymphal population dynamics in 1998, 1999 and 2000 (Figs 2, 3) showed typical and consistent population dynamics for the Bordeaux region (Decante & van Helden, 2006). Abundance in 1998 systematically exceeded that recorded in 1999 and 2000. For all years, the A0 peak (week 13–22) was clearly separated from those of the overlapping A1 and A2 (adult summer generations, week 22–39). Similarly, the N1 peak (first nymphal generation, week 19–25) was clearly separated from the N2 peak (second nymphal generation, week 25–36). In 1999 (Fig. 2B), two successive A0 peaks were observed during plot colonization and two moderate A1 peaks were clearly separated from a single more prominent A2 peak.

Aggregation levels I_a of weekly SpDs

Significantly aggregated SpDs were frequently observed during summer generations. In 1998 and 2000, aggregated adult SpDs occurred mainly at the end of summer generations (during A2; Fig. 2, weeks 30–36) whereas, in 1999, such aggregated SpDs appeared earlier and for a shorter period (end of A1, weeks 28–29). SpDs aggregation levels were greatest in N2 (up to 3.1) with respect to other stages and generations. Finally, significantly aggregated SpDs were rarely observed in between population peaks.

Temporal consistency X of weekly SpDs

Indices of association X revealed significantly positive associations between consecutive SpDs within N2 population peaks (Fig. 3) and, to a lesser extent, within A1–2 population

Table 2 Association levels among average spatial distribution (AspD) (upper) and associated probabilities (lower), inside and over years

P/X	Association level X											
	98A0	99A0	00A0	98N1	99N1	00N1	98A1–2	99A1–2	00A1–2	98N2	99N2	00N2
Probability of association P												
98A0		0.00	–0.04	0.12	–0.02	0.32	0.24	0.07	0.06	0.06	–0.08	–0.01
99A0			–0.09	–0.21	–0.08	–0.05	0.09	–0.06	–0.03	0.25	0.22	0.24
00A0				0.08	–0.10	0.03	0.18	0.25	0.29	0.08	0.00	0.02
98N1	*				0.28	0.14	0.03	0.14	0.15	0.10	0.14	0.02
99N1				***		0.08	0.02	0.01	0.15	0.06	0.02	0.04
00N1	***			*			0.06	0.09	0.16	–0.08	0.09	–0.04
98A1–2	***		**					0.41	0.24	0.22	0.16	0.11
99A1–2			***	*			***		0.28	0.08	0.11	0.14
00A1–2			***	*		*	***	***		0.13	0.28	0.24
98N2		***					***		*		0.61	0.64
99N2		***		*			**	*	***	***		0.53
00N2		***						*	***	***	***	

*Significant association ($X > 0$: * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$) between AspDs.

peaks (Fig. 2), for all years. Associations between successive SpDs within A0 and N1 were irregular, and several significantly dissociated SpDs arose. SpDs associations arose between successive peaks (A0/A1–2, N1/N2) but were generally not significant. In 1999 (Fig. 2B), significant associations were recorded within each of the two successive A0 peaks, but not between them; association levels between consecutive SpDs of the two successive A1 peaks gradually increased; and association levels between consecutive SpDs of the prominent A2 peak gradually decreased.

ASpDs

Aggregations I_a of N2 ASpDs were systematically significant, whereas aggregations of ASpDs of other stages and generations were rarely significant (Table 1). Between-years comparisons of ASpDs of the same stage and generation systematically revealed significant associations for A1–2 and N2, but not for A0 or N1 (Table 2). Associations of A1–2 with N2 of the same year were significant in 1998 and 2000, but not in 1999. Associations between A0 and N1 ASpDs, and between N1 and A1–2 ASpDs, were generally not significant within the same year.

Variograms and cartography

Variograms for A1–2 and N2 ASpDs present similar characteristics every year (Fig. 4), and are consistent with the significant associations of these ASpDs over the years. A1–2 models are exponential (finite sill-bounded model), with moderate to high nugget effects. Models ranges were approximately 35–40 m. N2 models are a combination of exponential and power (infinite sill-unbounded model), with low nugget effects. The power component of the model, with infinite sill, reveals a more gradual spatial distribution of nymphs, and does not allow range quantification. However, the exponential component of the models indicates ranges of approximately 40–45 m.

Kriged maps (Fig. 5) confirmed the between-years similarities for A1–2 and N2 (Table 2; Fig. 4); patches and gaps clearly corresponded. Similarities between A1–2 and N2 SpDs of the same year are less perceptible on Kriged maps, probably because of difference in spatial structures (clustering level: Table 1; variogram models: Fig. 4; and cluster sizes: Fig. 5); adults were found in small and scattered clusters, whereas nymphs were more evenly distributed.

Discussion

Monitoring schedules and features of the plot largely influence the efficiency of such an analysis (Legendre & Fortin, 1989; Alexander *et al.*, 2005). On this flat and rather homogenous plot, weekly insect monitoring on 130 points revealed the fluctuating aggregation and association levels of the colonizing adults (A0) SpDs and those of their offspring (N1), as well as the more consistent SpDs of summer generations (A1–2 and even more N2).

The identified periods of consistent and rather stable SpDs for summer adults (A1–2) and very stable for summer nymphs (N2) justified their averaging. This circumvented the temporal autocorrelation problem, and allowed comparisons of spatial distributions between successive stages, generations and years, and the construction of variograms and maps. ASpDs of the rather stable A1–2 could be assessed with less frequent samplings, whereas those of nymphs could be performed through a single count per generation, at the population peak.

Low to moderate nugget effects observed in variograms of summer adult A1–2 and nymphs N2 (Fig. 4) indicate that sampling density (distance of 9×12 m between sampling points) allows an accurate spatial distribution map to be produced (Goovaerts, 1999). Moreover, an increase in YST density, which was considered so as to minimize nugget effects, would have led to visual interference among neighbouring chromo-attractive YSTs. By contrast, variograms ranges of summer

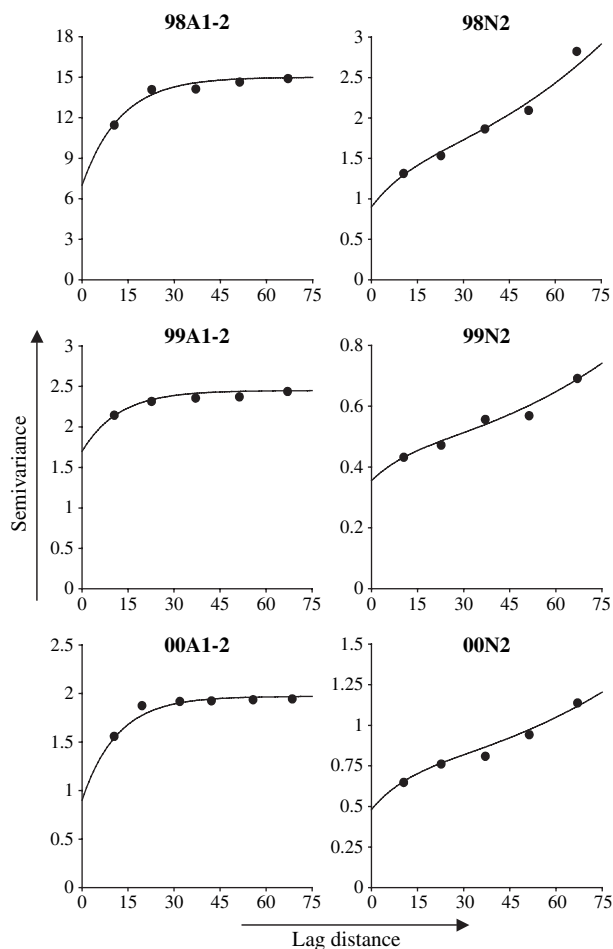


Figure 4 Average spatial distribution (AspD) variograms. Experimental omnidirectional variogram (●) and associated models (solid line) of summer adult (A1–2) and nymph (N2) AspDs.

adults and nymphs (35–45 m) largely exceeded the sampling density (9×12 m), thus indicating that the distance between sampling points could be increased, particularly on a more heterogeneous plot. Moreover, it would permit the extension of the studied area. Finally, the assessment of the relation between plot characteristics and *E. vitis* spatial distribution would probably benefit from a more heterogeneous plot.

In spring, the global lack of association among consecutive weekly trap catches (Fig. 2) revealed the dynamic nature of plot colonization. The expected influence of the presence of intermediate host plants on plot colonization (i.e. higher abundance at plot edges bordered by intermediate host plants) was not confirmed by spatial distribution maps (data not shown). The early peak observed in 1999 (before vine bud burst) indicates that overwintering adults forage for suitable host plants close to the vineyard (Decante & van Helden, 2006), whereas the second peak (after vine bud burst) corresponds to the actual colonization of the plot. The inconsistent A0 SpDs (Fig. 2) suggest that adults colonized the plot by successive flights, probably depending on the fluctuating weather conditions.

The generally low aggregation levels (Table 1), low between-years association (Table 2) and inconsistent spatial structures of A0 and N1 AspDs revealed by variograms (data not shown), all indicate random spatial distributions. Even though the abundance of N1 depends on those of A0, they presented different AspDs (Table 2). This was probably due to the dispersion phenomena identified for the mobile A0 rather than for the sedentary N1. However, differences in survival of eggs and nymphs, through biotic (e.g. natural enemies) or abiotic factors (e.g. temperature), could also explain the differences between A0 and N1 spatial distributions.

In summer, A1–2 SpDs were rather constant (Fig. 2) despite frequent migration events (Decante & van Helden, 2003, 2006), thus suggesting that the migrating adults rapidly redistributed inside the plot. A precise assessment of such an adult migration and re-distribution would require more frequent measurements. SpDs of the subsequent N2, which reflect the selection of egg-laying sites by adults, were even more aggregated and associated (Fig. 3).

Between-years comparisons of both A1–2 and N2 AspDs reveal high association levels (Table 2), similar variogram structures (Fig. 4) and spatial distributions (Fig. 5), supporting the hypothesis that perennial plot characteristics (biotic or abiotic) induce a similar spatial distribution of summer adults and nymphs each year.

Comparisons between the highly mobile A1–2 adults and their direct offspring, the rather sedentary nymphs N2, revealed highly significant associations in 1998 and 2000, and a weaker association in 1999 (Table 2). Even though the location of maximal and minimal population sizes was comparable, adults AspDs were more scattered (high nugget effects, finite sills), whereas nymphal AspDs were more gradual (low nugget effects, infinite sills) and significantly aggregated (Table 1). After their immigration, adults appear to disperse inside the plot, searching for vine plants suitable for egg-laying. This dispersion behaviour of adults of the successive immigration waves influences numbers trapped and could explain the inferior aggregation of adults A1–2 compared with those of their offspring N2. However, divergence in spatial distributions between summer adults and subsequent nymphs could also be explained by other processes (or a combination thereof). (i) It could be attributed to egg and nymph survival, which would vary across the plot because of the difference in the distribution of host plant characteristics related to egg and nymph survival (e.g. foliage microclimate, sap quality, etc.). (ii) The observed West–East gradient in nymphal AspD could also be attributed to natural enemies originating from woodlands (Cerrutti *et al.*, 1991; Boell & Hermann, 2004; Boeller *et al.*, 2004). However, observation of natural enemies (on traps or during counts) revealed neither gradual nor structured spatial distribution (data not shown). (iii) Finally, this divergence could also result from different spatial distribution for feeding-mating adults (both males and females) and for egg-laying adults (only females).

In conclusion our results revealed between-year similarities in spatial distributions of *E. vitis* summer generations. Evidence of a link between the sedentary summer nymphs and the highly mobile adults of the same year leads us to suggest

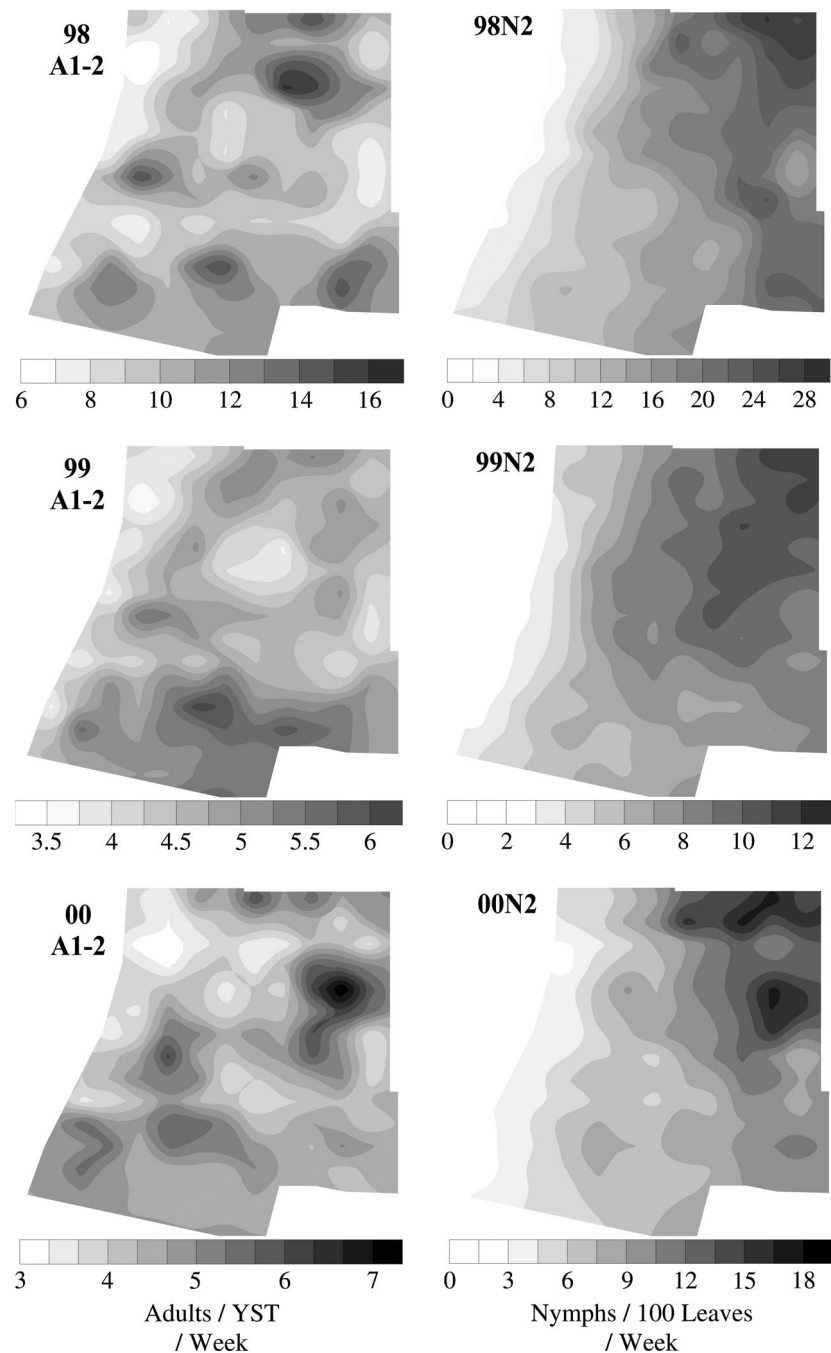


Figure 5 Average spatial distribution (AspD) distribution maps. Spatial distributions of summer adults (A1–2) and nymphs (N2) ASPDs are mapped using the Kriging method.

that these spatial distributions are related to some perennial spatial variability in plot characteristics. It may be that the gradual increase in nymphal abundance, from the western woodlands to the eastern plot edge, was due to a similar gradient of some plot characteristics influencing egg and nymph survival or selection of suitable egg-laying sites by adults. However, this may also result from the effects of natural enemies originating from these woodlands. Experiments should be conducted to confirm insect spatial distribution and to identify the related plot characteristics.

Acknowledgements

This work was funded by the ‘Conseil Interprofessionnel des Vins de Bordeaux (CIVB)’ and the ‘Vignobles Bardet’. We thank Bernard Chauvin, Gaëlle Denier and all the students who participated; Philippe Bardet and Eric Fargeot for their help with our trapping systems and samplings; Olivier Lavialle, Jean-Pierre Rossi and Pascal Monestiez for their advice on statistical methods; and Daciana Papura and Lee Valente for their help in writing the manuscript.

References

- Alexander, C.J., Holland, J.M., Winder, L., Woolley, C. & Perry, J.N. (2005) Performance of sampling strategies in the presence of known spatial patterns. *Annals of Applied Biology*, **146**, 361–370.
- Backus, E.A., Serrano, M.S. & Ranger, C.M. (2005) Mechanisms of hopperburn: an overview of insect taxonomy, behavior, and physiology. *Annual Review of Entomology*, **50**, 125–151.
- Baillod, M., Jermini, M., Antonin, P., Linder, C., Mittaz, C., Carrera, E. & Udry, V. (1993) Stratégies de lutte contre la cicadelle verte de la vigne, *Empoasca vitis* (Goethe). Efficacité des insecticides et problématique liée à la nuisibilité. *Revue Suisse de Viticulture, Arboriculture et Horticulture*, **25**, 133–141.
- Baudry, O., Bourger, C., Guyot, G. & Rieux, R. (2000) *Les haies composites réservoirs d'auxiliaires*. CTIFL, France.
- Baur, R., Remund, U., Kauer, S. & Boeller, E.F. (1998) Seasonal and spatial dynamics of *Empoasca vitis* and its egg parasitoids in vineyards in Northern Switzerland. *IOBC-WPRS Bulletin*, **21**, 71–72.
- Boell, S. & Hermann, J.V. (2004) A long-term study on the population dynamics of the grape leafhopper (*Empoasca vitis*) and antagonistic mymarid species. *Journal of Pest Science*, **77**, 33–42.
- Boeller, E.F., Häni, F. & Poehling, H.M. (2004) *Ecological infrastructures: ideabook on functional biodiversity at the farm level - temperate zones of Europe*. IOBC/WPRS Commission on Integrated Production Guidelines and Endorsement, Germany.
- Bosco, D., Alma, A., Bonelli, S. & Arzone, A. (1996) Phenology and within-vineyard distribution of *Empoasca vitis* Goethe adults (Cicadellidae Typhlocybinae). *Redia*, **79**, 1–9.
- Bramley, R.G.V. (2005) Understanding variability in winegrape production systems: 2. Within vineyard variation in quality over several vintages. *Australian Journal of Grape and Wine Research*, **11**, 33–42.
- Bramley, R.G.V. & Hamilton, R.P. (2004) Understanding variability in winegrape production systems: 1. Within vineyard variation in yield over several vintages. *Australian Journal of Grape and Wine Research*, **10**, 32–45.
- Candolfi, M.P., Jermini, M., Carrera, E. & Candolfi-Vasconcelos, M.C. (1993) Grapevine leaf gas exchange, plant growth, yield, fruit quality and carbohydrate reserves influenced by the grape leafhopper *Empoasca vitis*. *Entomologia experimentalis et applicata*, **69**, 289–296.
- Cerutti, F., Baumgartner, J. & Delucchi, V. (1991) The dynamic of grape leafhopper *Empoasca vitis* Goethe populations in southern Switzerland and the implications for habitat management. *Biocontrol Science and Technology*, **1**, 177–194.
- Corino, L., Ruaro, P. & Abate, R. (1992) La cicadelle de la vigne *Empoasca vitis* Guethe (Homoptera, Cicadellidae, Typhlocybinae): étude de la biologie dans une région viticole du piémont. *IOBC-WPRS Bulletin*, **15**, 40.
- Decante, D. & van Helden, M. (2006) Population ecology of *Empoasca vitis* (Goethe) and *Scaphoideus titanus* (Ball) in Bordeaux vineyards: influence of migration and landscape. *Crop Protection*, **25**, 696–704.
- Decarte, D. & van Helden, M. (2003) Green leafhopper (*Empoasca vitis* Goethe) migrations and dispersions. *IOBC-WPRS Bulletin*, **26**, 189–196.
- Delbac, L., Fos, A., Lecharpentier, P. & Stockel, J. (1996) Confusion sexuelle contre l'Eudemis: impact sur la cicadelle verte dans le vignoble bordelais. *Phytoma-LDV*, **488**, 36–39.
- Della Giustina, W. (2002) Les cicadelles nuisibles à l'agriculture le partie. *Insectes*, **126**, 3–6.
- DeLong, D.M. (1971) The bionomics of leafhoppers. *Annual Review of Entomology*, **16**, 179–210.
- Dutilleul, P. (1993) Modifying t test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.
- Emmen, D.A., Fleischer, S.J. & Hower, A. (2004) Temporal and spatial dynamics of *Empoasca fabae* (Harris) (Homoptera: Cicadellidae) in Alfalfa. *Environmental Entomology*, **33**, 890–899.
- Fos, A., Delbac, L., Lecharpentier, P., Lecharpentier, V. & Stockel, J. (1997) Etude de la répartition spatiale d'*Empoasca vitis* Goethe (Homoptera, Typhlocybinae) et apports pour l'échantillonnage. I – Répartition sur le cep de vigne. *Journal International des Sciences de la Vigne et du Vin*, **31**, 119–125.
- Genini, M. (2000) Antagonistes de la cicadelle verte et des vers de la grappe dans le vignoble valaisan et les milieux environnants. *Revue Suisse de Viticulture, Arboriculture et Horticulture*, **32**, 153–160.
- Goovaerts, P. (1999) Geostatistics in soil science: state-of-the-art and perspectives. *Geoderma*, **89**, 1–45.
- van Helden, M., Decante, D. & Papura, D. (2003) Possibilities for conservation biological control against grape pests in the Bordeaux region. *IOBC-WPRS Bulletin*, **26**, 191–196.
- Holt, J., Chancellor, T.C.B., Reynolds, D.R. & Tiongco, E.R. (1996) Risk assessment for rice planthopper and tungro disease outbreaks. *Crop Protection*, **15**, 359–368.
- Irwin, M.E. (1999) Implications of movement in developing and deploying integrated pest management strategies. *Agricultural and Forest Meteorology*, **97**, 263–274.
- Ishii-Eitman, M.A. & Power, A.G. (1997) Response green rice leafhoppers to rice-planting practices in northern Thailand. *Ecological Applications*, **7**, 194–208.
- Jeger, M.J. (1999) Improved understanding of dispersal in crop pest and disease management: current status and future directions. *Agricultural and Forest Meteorology*, **97**, 331–349.
- Lamp, W.O. & Zhao, L. (1993) Prediction and manipulation of movement by polyphagous highly mobile pest. *Journal of Agricultural Entomology*, **10**, 267–281.
- Legendre, P. & Fortin, M. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–138.
- Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their function and interactions with agriculture. *Agriculture, Ecosystems and Environment*, **89**, 5–21.
- Matsumura, M. & Suzuki, Y. (2003) Direct and feeding-induced interactions between two rice planthoppers, *Sogatella frugifera* and *Nilaparvata lugens*: effects on dispersal capability and performance. *Ecological Entomology*, **28**, 174–182.
- Orenstein, S., Zahavi, T., Nestel, D., Sharon, R., Barkalifa, M. & Weintraub, P.G. (2003) Spatial dispersion patterns of potential leafhopper and planthopper (Homoptera) vectors of phytoplasma in wine vineyards. *Annals of Applied Biology*, **142**, 341–348.
- Perry, J.N. & Dixon, P.M. (2002) A new method to measure spatial association for ecological count data. *Ecoscience*, **9**, 133–141.
- Perry, J.N., Winder, L., Holland, J.M. & Alston, R.D. (1999) Red-blue plots for detecting clusters in count data. *Ecology Letters*, **2**, 106–113.
- Rousseau, J. (1994) La cicadelle verte, un équilibre écologique à préserver. *Alter Agri*, **11**, 27–29.
- Taylor, J.A. (2005) *Digital Terroirs and Precision Viticulture: Investigations into the Application of Information Technologies in Australian Vineyards [e-book]*. Australian Centre for Precision Agriculture, Australia [WWW document]. URL http://www.usyd.edu.au/su/agric/acpa/people/james/Thesis/PhD_Taylor_2004.pdf. [Accessed March 2007]
- Taylor, R.A.J. (1985) Migratory behaviour in the Auchenorrhyncha. *The Leafhoppers and Planthoppers* (ed. by L. R. Naullt and J. G. Rodriguez), pp. 259–288. Wiley and Sons, New York, New York.
- Vidano, C., Arno, C. & Alma, A. (1987) On the *Empoasca vitis* intervention threshold on vine (Rhynchota Auchenorrhyncha). *Proceedings of the Sixth Auchenorrhyncha Meeting* (ed. by C. Vidano and A. Arzone), pp. 525–537. Centro Nazionale delle Ricerche, Incremento Produttività Risorse Agricole, Italy.

Accepted 21 September 2007