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# Influence of plot characteristics and surrounding vegetation on the intra-plot spatial distribution of *Empoasca vitis*

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- Abstract**
- 1 Spatial distributions of adults and nymphs of *Empoasca vitis* were assessed during 3 years inside two adjacent vine plots having considerable intra-plot variability, diversified natural ground cover and surrounding vegetation, and no insecticide application.
  - 2 Geostatistical analysis confirmed that, in spite of repeated adult migrations, spatial distributions of summer populations were highly aggregated, similar every year and similar between adults and nymphs. Comparison of insect distribution with intra-plot characteristics, such as vine plant vigour (leaf density and leaf chlorophyll concentration) and phenology, plot topography and surrounding vegetation, revealed that *E. vitis* clearly aggregates in areas with the most vigorous vine plants.
  - 3 Even though the presence of natural enemies in the surrounding vegetation was confirmed by specific observations, we did not observe significant population decrease at the contiguous plot edges. Natural ground cover, together with the absence of insecticide, might allow the spreading and perennial conservation of *E. vitis* natural enemies inside the plots.
  - 4 Clear adult aggregations observed along downwind woodlands suggest that this vegetation acts as a barrier and intercepts the adults flying passively across the plot. However, this surrounding vegetation could also serve as an alternative refuge when vine water deficit and vine foliage temperature increase.

**Keywords** Aggregation, cicadellidae, migration, spatial distribution, viticulture.

## Introduction

In perennial crops, such as vineyards, local differences in factors such as soil, climate, topography and surrounding vegetation are the source of notable intra-plot variability of host plant characteristics, which appears to be rather consistent between years (Bramley & Hamilton, 2004; Bramley, 2005). Such intra-plot variations of plant characteristics can influence the spatial distribution (SpD) of pests and natural enemies, as observed on other crops (Schotzko & Smith, 1991; Holland *et al.*, 2004, 2005). Moreover, the SpD of pests is likely to be influenced by the plot surroundings (Hunter, 2002), either because this vegetation is a reservoir for pests (through the presence of alternative host plants; Holland & Fahrig, 2002) or for their antagonists (i.e. natural enemies: Altieri & Nicholls, 2002; Boeller *et al.*, 2004; Pollard & Holland, 2006). This surrounding vegetation can also constitute a physical obstacle

for insects' movements (Thomas *et al.*, 2001; Marshall, 2002; Wratten *et al.*, 2003).

Precise knowledge of the ecology and SpD of pests, and the relation to the characteristics of agro-ecosystems, could help to improve Integrated Pest Management (IPM) practices (i.e. population monitoring, farmscaping, reduction of pesticide application, etc.). Precision agriculture (i.e. low-cost positioning systems, crop measurement devices and reliable devices to store and share information) offers possibilities for finer (intra-plot) agricultural management. The recent extension of precision agriculture to viticulture (Hall *et al.*, 2002; Taylor, 2005; Tisseyre *et al.*, 2006), combined with better knowledge of pest SpD, could enhance vineyard management and protection.

Migrations constitute an important characteristic of leafhoppers (Hemiptera: Auchenorrhyncha) biology (DeLong, 1971; Taylor, 1985; Della Giustina, 2002). This is not limited only to an effect on their population dynamics in agricultural plots. Active movements should also have an effect on their SpD and might result in aggregations inside optimal habitat areas.

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The green leafhopper *Empoasca vitis* (Goethe), a European vine pest, induces leaf necrosis as a consequence of phloem punctures (hopperburn: Backus *et al.*, 2005). Outbreaks of this polycyclic pest (two to four generations per year) occasionally provoke delayed maturity and reduced berry sugar content (Vidano *et al.*, 1987; Candolfi *et al.*, 1993; Delbac *et al.*, 1996). *Empoasca vitis* shows several migratory phases. In spring and autumn, adults migrate over short distances from and to the surrounding vegetation where they overwinter (Decante & van Helden, 2006). In summer, massive migrations are also observed (Genini, 2000; Decante & van Helden, 2003, 2007) but the origins and distances of these migrations remain undetermined. Despite repeated adult migrations above vine foliage and passive transport in dominant winds (Decante & van Helden, 2003), SpDs of summer adults and nymphs inside an homogenous plot (flat, planted with the same variety) are rather aggregated and constant in the same year and between years (Decante & van Helden, 2007). Therefore, it can be assumed that the intra-plot *E. vitis* SpD is based on microhabitat differences resulting from the variability of some 'perennial' biotic and abiotic factors of the plot and its surroundings.

Such perennial variability of intra-plot characteristics has rarely been taken into account for SpD studies of *E. vitis*, but several factors can be considered to be important. Mayse *et al.* (1991) and Daane and Williams (2003), respectively, have shown the effect of nitrogen fertilization and irrigation of vineyards on the distribution of the variegated leafhopper *Erythroneura variabilis* (Beamer). Vine nitrogen and water status vary within vineyards (Goutouly *et al.*, 2006; van Leeuwen *et al.*, 2006, 2007; Tisseyre *et al.*, 2006) and could influence food or habitat quality for *E. vitis*. *Empoasca vitis* is vulnerable to temperatures above 32 °C (Cerutti *et al.*, 1991), which can be surpassed in the case of water deficit stress, inhibiting foliage transpiration and cooling.

A great variety of 'edge effects' on the intra-plot *E. vitis* SpD is assumed in the literature. A gradual reduction of *E. vitis* populations, through increased presence of natural enemies [mainly the Mymaridae egg-parasitoid *Anagrus atomus* (Haliday) Hymenoptera: Mymaridae], from plot edges bordered by hedges and woodlands to the core area of the plot, is often suggested (Baur *et al.*, 1998; Boeller *et al.*, 2004). However, the range and impact of natural enemies coming from outside the crop are not clearly quantified (Genini, 2000; Altieri & Nicholls, 2002; Sentenac, 2005a, b; van Helden *et al.*, 2006). A direct influence of plot borders on *E. vitis* could also result from the presence of alternative host plants (van Helden *et al.*, 2003; Decante & van Helden, 2006, 2007) or, more generally, through the presence of alternative food sources (i.e. supplementation). The polyphagous *E. vitis* present on plot borders might leave vine plants and take refuge in neighbouring vegetation in summer and autumn (Bosco *et al.*, 1996). These 'edge effects' could also be attributed to the influence of neighbouring vegetation on climate or plant quality inside plots (e.g. shade, water deficit stress).

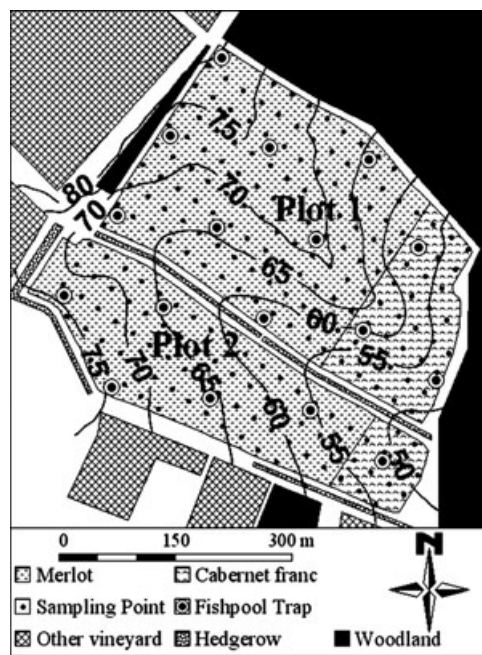
To identify the origins of such perennial aggregations, *E. vitis* SpD was compared with vine-plant vigour and phenology, plot topography and surrounding vegetation across a large plot, with notable variability being demonstrated in these characteristics. Knowledge of their impact on the *E. vitis* SpD could

improve knowledge of the insect's eco-ethology and, consequently, optimize monitoring and IPM methods. Possibilities for IPM improvement, through habitat management (Boeller *et al.*, 2004), as well as 'precision pest management' (i.e. pesticide spraying adjusted to plot characteristics), through the measurement of vineyard characteristics at the intra-plot scale (Taylor, 2005; Tisseyre *et al.*, 2006), are considered further in the present study.

## Materials and methods

### Vineyard

The study took place in the 'Cotes-de-Castillon' area of Bordeaux vineyards (France) on two neighbouring vineyard plots of 11.6 ha (plot 1) and 6.7 ha (plot 2), separated by a small stream bordered with mixed low (< 2 m) hedgerows (Fig. 1). Both were planted in 1970 at 3333 plants/ha (3 × 1 m spacing), with *Vitis vinifera* cv. Merlot on the north-western part (plot 1: 8.8 ha to plot 2: 5.8 ha) and Cabernet franc on the south-eastern part (plot 1: 2.8 ha to plot 2: 0.9 ha). Vine rows were orientated on a 34–214° axis, approximately parallel to the steepest slope. The larger plot includes two opposite slopes (north-eastern and south-western exposition, up to 30 m of amplitude) on each side of a ridge, whereas the smaller was planted on a south-western slope. Plots had permanent natural ground cover and were surrounded by woodlands, mixed hedges and other vine plots. Vine plants were 'double guyot' pruned and the training system comprised vertical shoot positioning. At full vegetation, foliage trimming of approximately 40 cm in width was performed between 0.5 (stem height) and 2.0 m (top of canopy). Plots



**Figure 1** Map of the studied plot: varieties and trapping devices of the experimental plots, surrounding vegetation (woodlands, hedgerows and vineyards) and topography (contour line of altitude in meter).

were dedicated to wine production and managed according to integrated farming standards. They had received no insecticide after 1998, thus allowing for reliable measurements of the *E. vitis* SpD.

### Data collection

All measurements were performed from April 2001 to November 2003 on a regular ( $27 \times 30$  m) sampling grid (9 rows  $\times$  30 plants), with 225 measuring points (plot 1: 146 measuring points = 113 Merlot + 33 Cabernet franc; plot 2: 79 measuring points = 66 Merlot + 13 Cabernet franc; Fig. 1).

### Spatial distribution of *E. vitis*

Adult and nymphal SpD were assessed yearly during the entire vine growing season. They are referred to throughout the text by the year number (01-02-03), followed by 'A1-2' for adults or 'N2' for nymphs.

**Adults:** one Yellow Sticky Trap (YST; Biosystemes France, France) of  $5 \times 15$  cm per measuring point was fixed on the highest trellis wire, in the upper part of the vine canopy (height 2 m). Adults were counted and the YSTs changed every 2 weeks. Adult counts were averaged over 12 weeks during the summer population peaks, as in Decante and van Helden (2007). Adult abundance is expressed as average number of adults per YST per week.

To assess adult dispersion and migration, 17 'Fishpool traps' (Fishpool *et al.*, 1988) (i.e. vertical tubes; height 5 m, diameter 15 cm) that support circular YST (height 10 cm) at several heights were placed between rows (Fig. 1) and monitored simultaneously. A detailed description of the trapping device and the results obtained is provided elsewhere (Decante and van Helden, 2003).

**Nymphs:** nymphs were counted once per generation, 3 to 4 weeks after the first trapping peak of summer adults. Nymphs were counted beside each YST, on 40 mature leaves (Vidano *et al.*, 1987; Fos *et al.*, 1997), selected randomly on five consecutive vine plants. Nymph abundance is expressed as the number of nymphs per 100 leaves.

### Characteristics of the plot

Characteristics of the plot and the surrounding vegetation were assessed on each measuring points of the sampling grid. Detailed features of the methods employed are presented in Table 1.

**Vine plant characteristics:** vigour, phenology and water deficit stress of vine plants were assessed at each measuring point (Table 1), on five consecutive plants (the same used for counting nymphs, see above). Vigour was measured yearly through two distinct indicators: leaf chlorophyll concentration, using the Norsk Hydro N Tester (Norsk Hydro ASA, Norway) and foliage density, estimated as the pruning wood weight. Phenology of the vine plants was estimated yearly by counting number of leaves per growing shoot in spring. Intensity of water deficit stress was measured only in 2003, using the  $\delta^{13}\text{C}$

method. Finally, the vine plant variety corresponding to each measuring point (Fig. 1) was taken into account as a dummy variable.

**Topography:** the exact location of all measuring points, plot contour and location of neighbouring landscape elements were measured using a GPS (Leica GS50; Leica, Germany) and post-processing procedure (Leica GIS DataPro). These post-processed GPS data were used for kriging and to calculate altitudes and solar exposure of measuring points (i.e. slope inclination along the north-south axis; Fig. 1).

**Plot surroundings:** the shortest distances separating each measuring point both from plot edge and from downwind woodlands (i.e. northern woodlands; Fig. 1) were measured with post-processed GPS data. Measuring points were classified into two groups with respect to the distance from nearest plot edge, inferior (peripheral) or superior (core area) to 30 m, with a dummy variable.

### Statistical analysis

All statistical methods used for data analysis are similar to these previously described (Decante and van Helden, 2007).

#### Aggregation levels

Aggregation levels of SpDs of adults, nymphs (Table 2) and host-plant characteristics (data not shown) were calculated using the Spatial Analysis by Distance IndicEs method for spatial clustering (SADIE; Perry *et al.*, 1999). This measures the clustering indices ' $v$ ' of each sampling point, the overall degree of clustering in the data (in the form of patches and gaps) and the associated probability with a permutation test (2000 randomizations).

#### Variograms and cartography

Omnidirectional variograms were plotted and modeled for SpD of adults, nymphs and host-plant characteristics. Semivariances of variograms were calculated over distances of 210 m, with seven lags of 30-m increments. The resulting models were used to map the SpDs of adults, nymphs and host-plant characteristics using the Kriging method (Goovaerts, 1999).

#### Spatial association with plot characteristics

Association levels ( $X$ ) and probability for significant independence ( $p$ ) of adult and nymphal SpDs with the quantitative variables listed in Table 1 were calculated using the SADIE method for spatial association (Perry & Dixon, 2002). This 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 permutation test (2000 randomizations), allows comparison of data sets with any frequency distribution; and (iii) the amount of information in spatially autocorrelated

**Table 1** Abbreviation and methods used for the measurement of plot characteristics

Characteristic	Abbreviation	Method
Leaf chlorophyll concentration	NTEST	Optical measurement with the Norsk Hydro N Tester (Bavaresco, 1995; Spring, 1999; Spring & Zufferey, 2000) on 30 mature leaves on each side of the row during the <i>Empoasca vitis</i> summer population peak
Leaf density (pruning wood weight)	PWW	Estimated by total weight of annual pruning wood contained in a fixed volume of (trimmed) foliage during the ongoing year, and measured in the next winter (Champagnol, 1984; Goutouly <i>et al.</i> , 2006)
Precociousness of phenology (at bud break)	BDB	Estimated by average numbers of leaves per growing shoot, measured in spring, 4 weeks after bud break (Baggiolini stage E–F)
Water deficit stress ( $\delta^{13}\text{C}$ method)	WDS	Photosynthetic carbon isotope composition ( $^{12}\text{C}/^{13}\text{C}$ ratio) measured on grape must at maturity (Gaudillere <i>et al.</i> , 2002): integrative indicator of WDS during berry ripening period
Variety	VAR	Vine plant variety of the measuring point (dummy variable: 0 for Merlot, 1 for Cabernet franc)
Altitude	ALTI	Absolute altitude measured using post-processed GPS data
Solar exposure	SLOPE	Slope inclination measured in degree along the north–south axis (positive if exposed to south; negative if exposed to north), calculated with post-processed GPS data
Distance from plot edge	EDGE	Distance separating each measuring point from the nearest plot edge, calculated with post-processed GPS data
Edge effects	EDGE	Classification with respect to proximity to plot edge (dummy variable: 0 for core area of plots, 1 for plot periphery)
Distance from downwind woodlands	DWOOD	Shortest distance separating each measuring point from downwind (northern) woodlands, calculated with post-processed GPS data

data sets (i.e. where a value of one sampling point is not completely independent of its neighbours) is reduced. The resulting bias in probability  $P$  for significant association (or dissociation) between two autocorrelated data sets is accounted for by calculating a ‘scale factor’ (coefficient between the effective size of data sets and the actual number of sampling points) with the method of Dutilleul (1993). Probability for significant independence ( $p$ ) of adult and nymphs SpD with the categorical variables [edge (EDGE) and varieties (VAR)] were calculated on raw data using the Mann–Whitney  $U$ -test.

### Modelling

SpDs of plot characteristics showing significant dependence on adult or nymphal SpD every year were selected for multiple regression modelling through the progressive stepwise procedure (XLSTAT 4.2 software; Addinsoft, New York, New York). Because this procedure requires normally distributed data, quantitative variables (including *E. vitis* SpDs) were transformed using the Box–Cox method (Freeman & Modarres, 2005) and centered-reduced. The categorical variables (EDGE and VAR) were introduced in the regression as a dummy variable. These regression models were calculated separately for each year, as well as over all years. Association with plot characteristics and stepwise regression of adult and nymphal SpDs were also calculated for sub-samples comprising: (i) Merlot measuring points only (179 measuring points) and (ii) ‘core area’ measuring points only (distance >30 m from plot edge; 141 measuring points).

## Results

### Population dynamics of *E. vitis*

Population dynamics of *E. vitis* monitored on the plots studied in 2001 and 2002 presented characteristics similar to those observed from 1998 to 2000 on another plot in the Bordeaux area (Decante & van Helden, 2007). However, the particularly dry and hot summer of 2003 strongly reduced the abundance of *E. vitis*; summer adults A1–2 were only slightly reduced, but summer nymphs N2 were almost absent, making a valid estimate of nymphal SpD impossible.

### Spatial distribution of *E. vitis*

Nymphal SpDs were significantly aggregated, confirming previous results (Decante & van Helden, 2007). In the present study, however, the aggregation of adult SpDs was also significant, and largely exceeded those of nymphs (Table 2). Adult and nymph variograms (Fig. 2) displayed consistent spatial structures fitting with exponential models, with moderate to high nugget effects (25–50% of the total semivariance) and ranges between 40–70 m.

Both adult and nymphal SpDs presented clear spatial associations between years. Moreover, SADIE X (Table 3) revealed substantial similarities between adult and nymphal SpDs of the same year (Fig. 3): locations of gaps (minimal abundance) clearly correspond, whereas population patches (maximal abundance) do not match exactly. If both adult and nymphs aggregate down the slopes, adults also aggregate in the northern part of the plot, alongside woodlands (Fig. 3).



**Table 2** Adult average spatial distribution periods (A1-2), nymph counting dates (N2) (ISO week numbers) and associated indices of aggregation  $I_a$  (in parentheses)

	A1-2	N2
2001	24–36 (3.2*)	31 (2.0*)
2002	24–36 (3.9*)	31 (1.7*)
2003	21–33 (2.5*)	

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

### Plot characteristics

Topography and plot surroundings were constant over the years (Fig. 1). Pruning wood weight (PWW) and leaf chlorophyll concentration (NTEST) distribution maps (Fig. 4) revealed rather constant SpDs over the 3 years. Clear differences for these two characteristics were observed between the Merlot and Cabernet franc areas; Merlot has lower PWW values and higher NTEST values than Cabernet franc. By contrast, precociousness of phenology (at bud break; BDB) presents rather inconstant SpDs between years. Variety differences of BDB were observed as expected between the 'early budding' Merlot and the 'late budding' Cabernet franc. However, unexpected (higher) BDB values were observed on the Cabernet franc in 2003, and to a

lesser extent in 2001. During these 2 years, spring frost damage occurred on the already growing Merlot vine plants but not on the still dormant Cabernet franc, resulting in a delay in growth stage. By contrast to vigour, lower BDB values were generally observed down the slopes. Despite a particularly hot and dry summer in 2003, the water deficit stress measurement revealed only weak to moderate stress. SpD of water deficit showed higher stress ( $\delta^{13}C > -26$ ) in the upper parts of the plot (Fig. 4).

### Relation between *E. vitis* SpD and plot characteristics

#### Multiple testing

When accounting for spatial autocorrelation (Legendre, 1993; Legendre *et al.*, 2002) with SADIE X (Perry & Dixon, 2002; Table 4), few significant relationships were observed. Adult and nymphal SpDs systematically showed significant positive associations with vigour (PWW and to a lesser extent NTEST) measured in the same year, and with south-exposed slopes (EXPO). Phenology (BDB), altitude (ALTI) and varieties (VAR) did not always show a significant spatial association with adult or nymphal SpDs.

Significant EDGE effects were rarely observed (Table 4). However, strong positive associations were observed between distance from downwind woodlands (DWOOD) and adult SpDs. By contrast, nymphal SpDs showed positive associations with distance from plot edge (DEDGE) but negative associations with distance from downwind woodlands (DWOOD).

#### Multiple regression modelling

The results obtained when introducing the selected characteristics (i.e. significantly related every year) into a progressive stepwise procedure are shown in Table 5. Vigour (PWW and to a lesser extent NTEST) clearly prevailed over all other characteristics for all (adult and nymphal, annual or bi-annual) models. Adult and nymphal models systematically take into account EXPO but its influence is inconsistent (negative in 2001 and 2003, positive in 2002). DWOOD is also systematically taken into account for adult models, and appears to explain a large part of adult SpD (Table 5). By contrast, nymphal SpD appears to be more influenced by DEDGE than DWOOD but the influence of these two characteristics is opposite. These models explain approximately 49% of adult SpD and 32% of nymphal SpD.

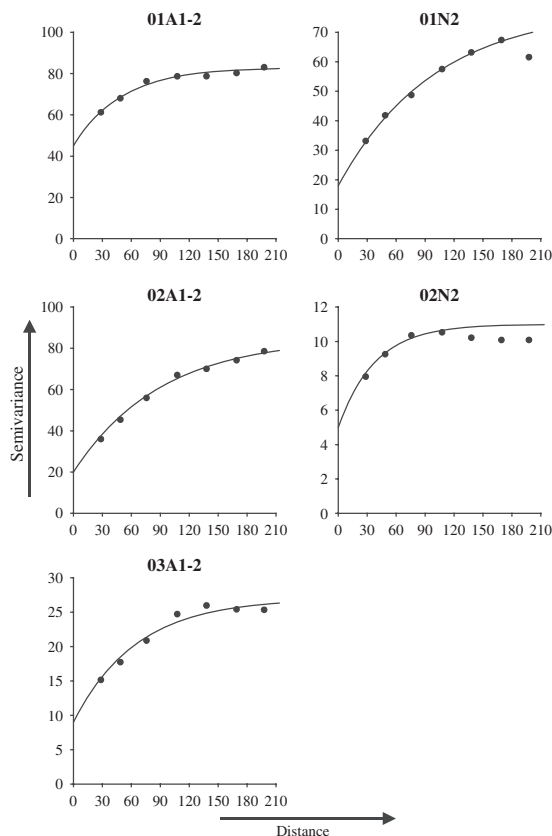
Despite a reduced number of measuring points in the Merlot or the core area subsets (Table 5), the resulting sub-models showed equivalent or slightly higher accuracy (adjusted  $r^2$ ). However, both sub-models had compositions (selected variable and correlation coefficients) very similar to that of the integral model.

## Discussion

### Methodology

#### Choice of the plot and monitoring methods

An initial study (Decante & van Helden, 2007) revealed highly aggregated and stable *E. vitis* SpD during summer, despite a



**Figure 2** Variograms: experimental omnidirectional variogram (●) and associated models (solid line) of summer adults (A1-2) and nymphs (N2).

**Table 3** Spatial association (SpD) *X* over *Empoasca vitis* SpDs and associated scale factors (in parentheses)

	01A1-2	02A1-2	03A1-2	01N2
02A1-2	0.62* (1.03)			
03A1-2	0.51* (1.04)	0.52* (1.12)		
01N2	0.40* (1.05)	0.39* (1.12)	0.22* (1.18)	
02N2	0.43* (1.02)	0.36* (1.02)	0.24* (1.09)	0.34* (1.08)

\*Significant association (probability of independence <0.05).

rather homogenous plot (flat, single variety) and massive adult immigrations (Decante & van Helden, 2003). For the present study, the plot was chosen so as to contain higher intra-plot variability, aiming to allow a better chance of identifying the origins of such 'perennial aggregations'.

The earlier results (structured *E. vitis* SpD, with moderate nugget effects and ranges that largely exceed the distance between measuring points) allowed us to reduce the density of the insect sampling network and thus to extend it to a larger plot. The stability of nymphal SpD justified reducing the nymphal counts (only one count at peak level versus weekly counts). The results obtained in the present study validate these choices. The only remarkable difference concerns the size of

the insect 'clusters', measured through variogram ranges. They reach up to 70 m (Fig. 2), most likely because the contrasted spatial structures of the influential plot characteristics were observed on a larger scale.

#### Statistical methods

Even though statistical tests lead to ascertaining an association between two variables, they do not demonstrate any causal–consequential relationship. However, the perennial stability (within and between years) of *E. vitis* SpD leads us to postulate that plot characteristics do influence *E. vitis* SpD.

When assessing the dependence between SpD of two variables (*E. vitis* SpD and plot characteristics), spatial autocorrelation prohibits the use of classical statistical tests (i.e. Student's *t*-test; Legendre & Fortin, 1989; Legendre *et al.*, 2002). Several well-adapted methods (Dutilleul, 1993; Dutilleul *et al.*, 2000) circumvent this difficulty. Among these methods, the SADIE method (Perry & Dixon, 2002) also allows measurement of the aggregation of SpDs. In addition, probabilities for significant aggregation and association are assessed with permutation test, thus allowing the assessment of data sets with any frequency distribution.

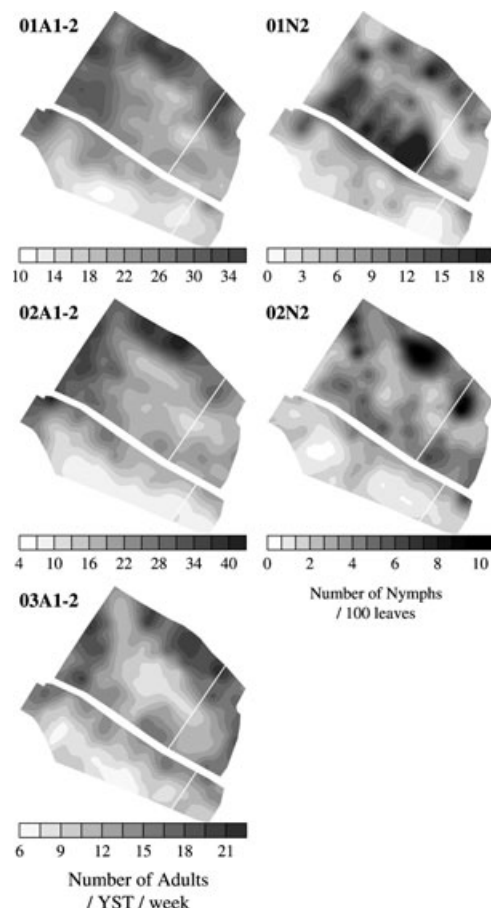
The paired comparison of one variable (e.g. *E. vitis* SpD) with each of the predictor variables (vigour, phenology, water deficit stress, solar exposure, topography, etc.) does not account for the inter-correlation among these (Table 4). The use of stepwise regression to discriminate among the characteristics significantly associated with *E. vitis* SpD improves the quantification of their respective influence (Table 5).

#### Eco-ethology of *E. vitis*

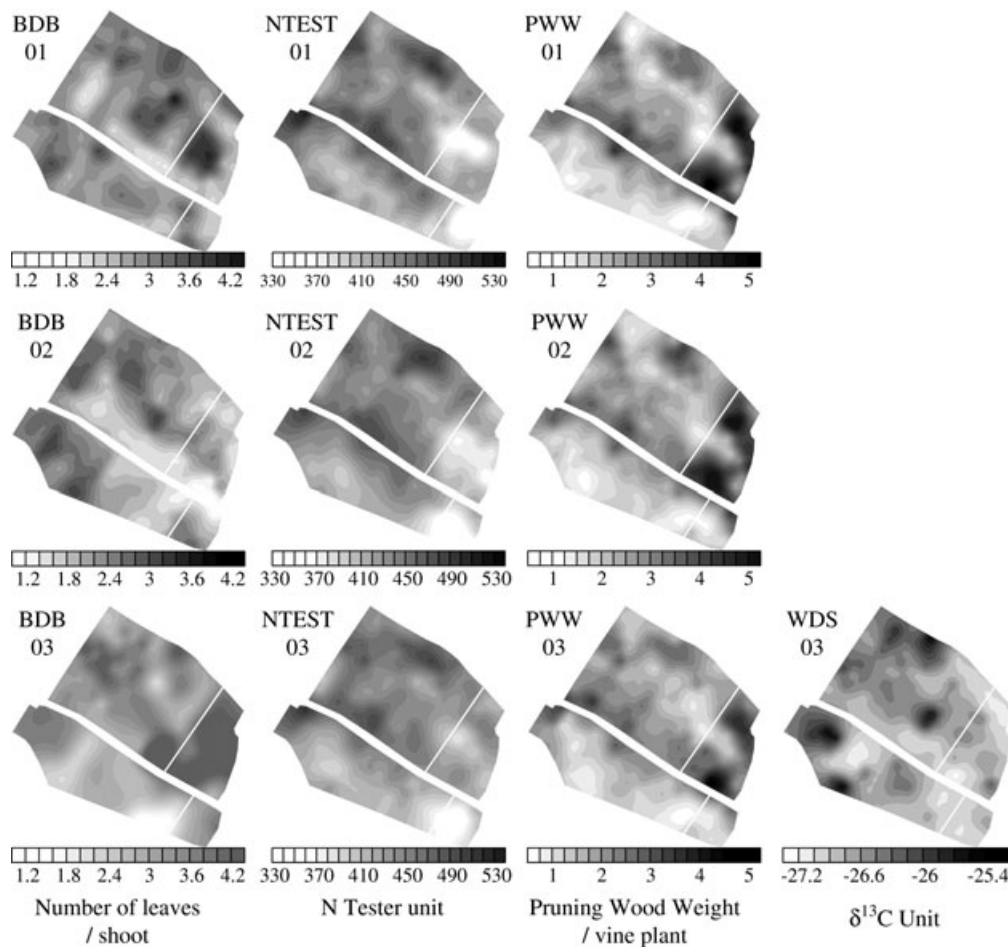
##### Influence of *E. vitis* migrations

Earlier observations (Decante & van Helden, 2003, 2006, 2007) strongly suggest that adults immigrate massively in summer, coming from different (unidentified) origins, and then disperse inside plots to the most suitable habitat areas (Bowman *et al.*, 2002).

Logically, SpD of the (sedentary) nymphs would reflect SpD of eggs and, by extension, the SpD of plot characteristics selected by adults for egg-laying. However, modelling of nymphal SpD indicates stronger association with plot characteristics than with adult (Table 5). The associations between adult trapping and nymph counts appear to suffer from several biases: (i) adult migration (and distribution) is influenced by the prevailing wind, whereas nymphs are sedentary; (ii) adult trap catches are influenced by abundance but also by their 'activity



**Figure 3** Distribution maps: spatial distributions of summer adults (A1-2) and nymphs (N2), mapped using the Kriging method.



**Figure 4** Annual distribution maps of vine plant characteristics: spatial distributions of precociousness of phenology (BDB), leaf chlorophyll concentration (NTEST) and leaf density (PWW) measured yearly are mapped using the Kriging method.

level'; (iii) adult trap catches consist of both males and females (often with more males than females) but only the females lay eggs; and (iv) the survival of eggs or young nymphs could vary across plots because of variations in abiotic factors, predation and parasitism, etc.

#### *Influence of plot characteristics*

Comparisons of plot characteristics with *E. vitis* SpD revealed several significant spatial associations. Even though they do not demonstrate any causal–consequential relationship, hypothesis of the mechanisms leading to such influence can be formulated.

**Table 4** Spatial association (SpD) *X* over *Empoasca vitis* SpDs and plot characteristics and associated scale factors (in parentheses)

		01A1-2	02A1-2	03A1-2	01N2	02N2
Host-plant characteristics	PWW	0.39* (1.08)	0.29* (1.10)	0.39* (1.24)	0.46* (1.26)	0.48* (1.10)
	NTEST	0.45* (1.02)	0.48* (1.12)	0.30* (1.11)	0.42* (1.23)	0.24* (1.02)
	BDB	0.10 (1.03)	0.15* (1.14)	0.13* (1.14)	–0.12 (1.17)	–0.15* (1.15)
	VAR				*	
Topography	ALTI	0.30* (1.17)	0.39* (1.22)	–0.04 (1.31)	–0.15 (1.39)	–0.02* (1.18)
	EXPO	0.37* (1.16)	0.35* (1.27)	0.21* (1.37)	0.45* (1.59)	0.26* (1.11)
Surrounding vegetation	DWOOD	–0.59* (1.06)	–0.58* (1.21)	–0.49* (1.37)	–0.22* (1.51)	–0.33* (1.08)
	DEGE	0.17* (1.00)	0.00 (1.26)	–0.16* (1.45)	0.23* (1.40)	0.21* (1.15)
	EDGE			*		

Significant association (probability of independence <0.05). Significant difference in population levels between varieties (categorical data) is tested by the Mann–Whitney *U*-test.

For abbreviations, see Table 1.



**Table 5** Parameters of the multiple stepwise regressions of the spatial association of *Empoasca vitis* on selected plot characteristics, with all measuring points (225: upper part), with Merlot measuring points only (179 measuring points) and with measuring points of the core area of the plot only (distance from plot edge >30 m; 141 measuring points)

		Year	Adjusted $r^2$	Regression coefficient				
				A1-2	PWW	NTEST	EXPO	DWOOD
All data 225	A1-2	2001	0.51		0.416	0.180	−0.044	−0.385
		2002	0.68		0.360	0.211	0.037	−0.522
		2003	0.36		0.431	0.114	−0.244	−0.242
Measuring points	N2	2001	0.36	0.109	0.306	0.132	0.229	−0.093
		2002	0.29	0.136	0.389	0.076	0.109	Ø
		2001–03	0.49		0.393	0.163	−0.081	−0.385
Merlot (179 MP)	N2	2001–02	0.32	0.105	0.352	0.102	0.171	−0.069
		2001–03	0.55		0.415	0.153	−0.114	−0.407
		2001–02	0.32	0.095	0.330	0.123	0.192	
Core area (141 MP)	A1-2	2001–03	0.50		0.448	0.140		−0.313
		2001–02	0.35	Ø	0.369	0.101	0.213	−0.187

Empty cells indicate parameters excluded by the multiple testing (i.e. not submitted to stepwise procedure); dashed circles Ø indicate parameters rejected by the stepwise procedure.

For abbreviations, see Table 1

Host plant characteristics: vigour (leaf density PWW and to a lesser extent chlorophyll concentration NTEST) was always positively associated with adult and nymphal SpDs, whereas phenology (BDB) was not (Table 4). Even though we observed a clear difference in vigour between grape varieties, the two models accounting for either ‘all measuring points’ or the Merlot measuring points only are similar (Table 5). These observations confirm that vigour prevails over all other characteristics, and can be considered as the key factor for *E. vitis* SpD.

Foliage density (PWW) appears to be the dominant vine plant characteristics for both adult and nymphs (Table 5). Moreover, the higher numbers of nymphs per leaf were observed on plants with higher numbers of leaves (higher PWW) corresponds to even higher numbers of nymphs per plant. The selection of plants with dense foliage by the egg-laying adults could be the result of more intense shade and evapotranspiration inside foliage, which together result in a cooler foliage microclimate (Champagnol, 1984; van Leeuwen *et al.*, 2006) more suitable for *E. vitis* (Vidano *et al.*, 1987; Fos *et al.*, 1997; Genini, 2000). Results obtained by Daane and Williams (2003) on *E. variabilis*, as well as the observed reduction of nymphal populations during the hot and dry summer of 2003, corroborate this theory.

Water deficit stress largely depends on canopy architecture and soil water holding capacity (i.e. soil depth and texture), which remain constant between years, and evaporative demand, which may vary between years and result in different stress intensity. However, the SpD of water deficit stress in 2003 may be representative of other years (van Leeuwen *et al.*, 2006). The results obtained in the present study showed no significant association between water deficit stress and adults SpD of the same year, and inconsistent associations with adult or nymphal SpDs of other years (data not shown). The nature of the  $\delta^{13}\text{C}$  method, an integrative indicator of water deficit stress during the berry ripening period, may not be adapted for comparison with adult and nymphal SpDs measured before

this period. Instead, simultaneous measurement of water deficit stress SpDs with direct methods, such as stem water potential or leaf temperature measurements by aerial photography, could be tested (van Leeuwen *et al.*, 2006).

The spatial association of chlorophyll concentration (NTEST) with *E. vitis* (mainly feeding on phloem; Boell *et al.*, 2005) could result from a combination of several characteristics (Fos *et al.*, 1997; Spring, 1999; Spring & Zufferey, 2000): (i) more intensive photosynthesis, resulting in a higher quality of phloem sap, (ii) more intensive green colour of vine leaves, resulting in visually more attractive plants; and (iii) leaf size and thickness, also correlated with plant vigour, resulting in variations of habitat quality for egg-laying. However, the latter characteristic seems less influential than PWW (Table 5).

Topography: the positive association between slope exposed to south (EXPO) and *E. vitis* SpDs (Table 4) was ambiguous. Adult models show a fluctuating contribution of EXPO (Table 5). The consistent contribution of EXPO to nymphal models (Table 5) could be related to the effect of solar exposure on photosynthesis intensity, vigour and temperature (Champagnol, 1984). However, this effect should be taken into account by the stepwise procedure (see Statistical methods).

#### *Influence of plot surroundings*

On adults: by contrast to Bosco *et al.* (1996), the results obtained in the present study do not show decreased adult trap catches at plot edges bordered by diversified vegetation (Tables 4 and 5). However, adult aggregations are mainly observed in the northern part of the plot, in the proximity of woodlands (Fig. 3). The substantial influence of DWOOD in all adult models, together with the passive transport of flying adults by the dominant wind (south to south-east) revealed by Fishpool trap monitoring (Decante & van Helden, 2003), suggests that adult aggregation could result from a ‘barrier effect’: interception of the migrating adults by high, dense vegetation such as woodlands. The resulting increased abundance of highly

active (migrating) individuals both contribute to increased trapping of adults along such plots edges, as observed by Genini (2000), Decante and van Helden (2003) and van Helden *et al.* (2003).

However, adult polyphagy, together with the affinity of *E. vitis* for cool and humid microclimates (Vidano *et al.*, 1987; Cerutti *et al.*, 1991), leads us to consider another hypothesis. Water deficit stress in late summer induces the increase in vine foliage temperature (van Leeuwen *et al.*, 2006), especially in the afternoon. Adults could leave vine plots to take refuge on host plants of the neighbouring woodlands, where the high and dense vegetation provides cooler shady areas, and returning to vine plots at night, when vine foliage temperature decreases.

On nymphs: the presence of natural enemies in woodlands and hedges surrounding the studied plots, as confirmed by specific monitoring (van Helden *et al.*, 2003), is expected to cause predation or parasitization of *E. vitis* eggs and nymphs at the plot border (Cerutti *et al.*, 1991; Genini, 2000; Altieri & Nicholls, 2002; van Helden *et al.*, 2003; Boeller *et al.*, 2004; Sentenac, 2005a, b). Even though our monitoring device was designed to trap *E. vitis*, we also trapped natural enemies. This monitoring did not reveal either an increased presence of natural enemies or a decreased presence of nymphs of *E. vitis* at plot edges (Fig. 3, Table 4). The natural groundcover of plots, together with the absence of insecticide application (subsequent to 1998), might have facilitated the spread and perennial conservation of natural enemies across the plot, thus masking possible edge effects.

The 'gradient' of natural enemies originating from the surrounding vegetation (through transects or networks covering extensive ranges) appears to be more adapted than when just considering 'edge effects' (comparing peripheral and core area of the plot). However, the nymphal SpD models (Table 5) reveal rather low, inconsistent and opposite influences of 'distance from plot edge' (DEDGE) and 'distance from downwind woodlands' (DWOOD). In our case, the prevailing influence of vigour on *E. vitis* SpD (i.e. on the whole plot scale) appears to interact with two effects of the surrounding vegetation: the 'barrier' effect and the 'natural enemies' effect.

## Prospects

Even though the present study permits a better comprehension of *E. vitis* eco-ethology, the results obtained mainly lead to a number of hypotheses that need to be tested by more specific experiments.

### *E. vitis* eco-ethology

The reason for the apparent preference of adults for high vigour remains unclear. Despite the recent results relating to feeding habits of *E. vitis* (Boell *et al.*, 2005) and other Typhlocybinae (Backus *et al.*, 2005), the influence of sap quality on *E. vitis* SpD can not be asserted. Similarly, the hypothesis of an influence of foliage temperature remains imprecise. Specific experiments, in particular tests of choice in controlled conditions, might shed light on the underlying mechanisms.

Knowledge of movements and migrations of *E. vitis* adults remains imprecise. As with closely-related Typhlocybinae (*Empoasca fabae* (Harris): Huff, 1963; Carlson *et al.*, 1992; Shields & Testa, 1999), these insects appear to perform long distance migrations (Decante & van Helden, 2006). The results obtained in the present study show that, despite such (passive) immigration, intra-plot dispersion occurs, resulting in a clearly aggregated distribution in preferred quality plot areas. This, and other fine-scale effects (physical barrier versus alternative refuge effects of woodlands) could be clarified using mark-capture techniques (Hagler & Jackson, 2001).

### Integrated pest management

When taken together with the results obtained in previous studies (Decante & van Helden, 2003, 2006, 2007; van Helden *et al.*, 2003), the results of the present study allow optimization of the IPM survey methods. Because the abundance of adults is significantly correlated with summer nymphs (Decante & van Helden, 2006), a potential nymph infestation could be anticipated by trapping adults, with a few YST distributed in the vigorous areas of the center of plots. In plots that present high adult trapp catches, nymphal counts should begin 2–4 weeks after the summer adult trapping peak (Decante & van Helden, 2006) in vigorous areas, and continue until the decrease in nymph abundance. Insecticide application should be carefully planned; natural enemies appear to play a major role in the regulation of *E. vitis* populations (Genini, 2000; Boeller *et al.*, 2004), and are vulnerable to insecticides.

The recent development of tools for 'precision viticulture' now permit the automated measurement of several vine plant characteristics. Aerial photography techniques allow straightforward measurements of both vigour and water deficit stress (Taylor, 2005; Goutouly *et al.*, 2006; van Leeuwen *et al.*, 2006; Tisseyre *et al.*, 2006). These methods should facilitate further studies on the impact of plot characteristics on pest SpD, and may, in the long term, lead to the development of 'precision pest management'. In particular, insecticide sprayings could be restricted to the certain areas of the plot (e.g. the most vigorous) and doses could take into account vine plant characteristics (e.g. leaf area, foliage density).

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