Spatial Distribution of Grape Root Borer (Lepidoptera: Sesiidae) Infestations in Virginia Vineyards and Implications for Sampling

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ABSTRACT Grape root borer, *Vitacea polistiformis* (Harris) (Lepidoptera: Sesiidae) is a potentially destructive pest of grape vines, *Vitis spp.* in the eastern United States. After feeding on grape roots for ≈2 yr in Virginia, larvae pupate beneath the soil surface around the vine base. Adults emerge during July and August, leaving empty pupal exuviae on or protruding from the soil. Weekly collections of pupal exuviae from an ≈1-m-diameter weed-free zone around the base of a grid of sample vines in Virginia vineyards were conducted in July and August, 2008–2012, and their distribution was characterized using both nonspatial (dispersion) and spatial techniques. Taylor's power law showed a significant aggregation of pupal exuviae, based on data from 19 vineyard blocks. Combined use of geostatistical and Spatial Analysis by Distance IndicEs methods indicated evidence of an aggregated pupal exuviae distribution pattern in seven of the nine blocks used for those analyses. Grape root borer pupal exuviae exhibited spatial dependency within a mean distance of 8.8 m, based on the range values of best-fitted variograms. Interpolated and clustering index-based infestation distribution maps were developed to show the spatial pattern of the insect within the vineyard blocks. The temporal distribution of pupal exuviae showed that the majority of moths emerged during the 3-wk period spanning the third week of July and the first week of August. The spatial distribution of grape root borer pupal exuviae was used in combination with temporal moth emergence patterns to develop a quantitative and efficient sampling scheme to assess infestations.

KEY WORDS *Vitacea polistiformis*, *Vitis vinifera*, geostatistics, SADIE, sampling

Grape root borer, *Vitacea polistiformis* (Harris), has been considered an economically important pest of grape vines, *Vitis* spp. in parts of the eastern United States for >150 yr (Harris 1854, Brooks 1907, Clark and Enns 1964, Pollet 1975, All and Dutcher 1978). The oligophagous larvae feed on the roots of commercially important *Vitis* spp. and rootstocks, causing extensive root damage that can lead to reduced vine vigor and productivity and eventual vine death in extreme cases (Clark and Enns 1964, Dutcher and All 1976, All et al. 1987). Adult females deposit ≈350–400 eggs (Brooks 1907, Dutcher and All 1978a) indiscriminately on the above-ground parts of vines and vegetation in vine rows over a period of 7–8 d after mating (Brooks 1907, Clark and Enns 1964, Dutcher and All 1979a). After hatching, neonates enter the soil to find and establish on vine roots, during which time their mortality is highest (Dutcher and All 1978b). In Virginia, larvae feed for ≈22 mo (reviewed in Bergh 2012) before leaving the root system to pupate beneath the soil surface around the vine base. Emerging moths leave an empty pupal exuviae at the soil surface, the presence and number of which provide an indication of the infestation status of individual vines.

Compared with many other insect pests of economically important crops, the development of a truly integrated approach for managing grape root borer has lagged significantly (reviewed in Bergh 2012). Importantly, there are no symptoms expressed by the above-ground parts of vines that can be unequivocally ascribed to the cumulative effects of grape root borer feeding on roots. Symptoms known collectively as "slow vine decline" (All et al. 1987), which include discolored and smaller leaves, reduced shoot growth, fewer and smaller berries, and vine wilting (Sorensen 1975, All et al. 1987), can be caused by grape root borer or a number of other horticultural or pathological conditions.

There are only two registered management options for grape root borer, soil drench applications of chlorpyrifos and mating disruption. In regions where grape root borer larvae have a 2-yr developmental period, managing an infestation requires implementing control measures in at least two consecutive seasons. In Virginia, chlorpyrifos is typically used as only a rescue treatment against severe infestations, creating a toxic barrier to neonates seeking roots in soil. However, many growers are reluctant to use chlorpyrifos in this manner because of perceptions of its negative impacts on soil biodiversity and associated effects on vine

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health, berry quality, and ultimately wine quality (Bergh 2012). Mating disruption, therefore, is currently the preferred option for managing grape root borer. Entomopathogenic nematodes have shown efficacy against this pest (Williams et al. 2010), but have not been widely adopted, largely because of the lack of coordinated efforts to educate growers about their use (Bergh 2012).

Another important and long-standing issue with grape root borer has been that most growers do not monitor or scout for this pest routinely, and thus remain unaware of infestations until vines begin to show symptoms of decline (Brooks 1907, Dutcher and All 1979b). It is often the case that infestations are detected only upon removal of affected vines and inspection of roots for larvae and their feeding channels. Researchers have monitored or assessed grape root borer populations using pheromone traps (Snow et al. 1987, Bergh et al. 2005), pupal exuviae counts (Johnson et al. 1991, Townsend 1991, Pearson 1992), and root inspection of extracted vines (Sarai 1972), although the latter is not often a pragmatic option. Captures of male grape root borer in pheromone traps accurately reflect the presence and seasonal phenology of adults, and have been used extensively for those purposes (Snow et al. 1991, Bergh et al. 2005, Weihman and Liburd 2007). However, no useful relationship has been found between the number of male moths captured in pheromone traps and pupal exuviae counts from individual vineyard blocks (J.P.R., unpublished data), likely because of the capture of moths emerging from other blocks and from wild vines (Snow et al. 1991, Webb et al. 1992, Bergh 2006). Consequently, the presence of pupal exuviae near the base of vines is the only unequivocal, nondestructive indicator of vine infestation by grape root borer larvae (Johnson et al. 1991, Bergh 2012).

Although an understanding of the spatial distribution of a pest species is crucial to the development of reliable sampling plans for estimating and predicting their densities and for implementing rational management decisions (Taylor 1984, Legendre and Fortin 1989, Liebhold et al. 1993), to our knowledge, the spatial distribution of grape root borer infestations has not been investigated, and its management has suffered from a lack of this basic information. Nonspatial techniques for studying insect distributions, using the relationship between mean and variance, have been used extensively to calculate dispersion indices (Southwood 1978, Taylor 1984, Kuno 1991, Young and Young 1998). However, the spatial patterns of insect densities can be characterized directly using geostatistical methods (Isaaks and Srivastava 1989, Rossi et al. 1992, Liebhold et al. 1993) that analyze and model the spatial relationships among individuals in a population (Schotzko and O'Keeffe 1990, Williams et al. 1992). Spatial dependence (autocorrelation) derived from geostatistical analyses can be used to predict populations at unsampled locations (e.g., by kriging), define sampling scales for independent samples, and to quantify the spatial pattern of insect species (Williams et al. 1992). The spatial distribution pattern of insect species can also be quantified using the method Spatial Analysis by Distance IndicEs (SADIE), which is particularly useful for count data (Perry 1995, Perry et al. 1999).

The objectives of this study were to characterize the distribution of grape root borer infestations in commercial vineyard blocks in Virginia, based on pupal exuviae sampling and the use of nonspatial and spatial techniques, and to develop a quantitative sampling plan for reliable and efficient assessment of the infestation status of individual vineyard blocks.

Materials and Methods

Study Sites and Pupal Exuviae Sampling. Grape root borer pupal exuviae were sampled from 48 vineyard blocks across 18 vineyards (geographic range: 38° 0′36″ N to 39° 19′12″ N and 77° 37′48″ W to 78° 50′60″ W) in Virginia. A vineyard block was defined as a portion of a vineyard within which the vines were essentially uniform in cultivar, rootstock, vine age, and other environmental and cultural practices. Each block was sampled once between 2008 and 2012. This sampling was part of another study that examined the factors associated with differences in the extent of grape root borer infestations among vineyards. For the study reported here, pupal exuviae data from 19 of the 48 blocks that met the following criteria were used for the analyses described below: 1) the block was large enough so that a grid of 80 sample points (vines) could be overlaid on the area and 2) the block ultimately yielded a seasonal mean of $\geq$0.1 pupal exuviae per vine. The 19 blocks selected were located in the following counties: Loudoun (2), Rappahannock (1), Shenandoah (4), Rockingham (3), Albemarle (6), and Nelson (3). The area sampled in each block ($\approx$ 0.4 ha) was a portion of a larger contiguous planting (1.86 $\pm$ 0.43 SE ha) of vines that were 11.8 $\pm$ 2.7 SE years old. Seven grape cultivars (Chardonnay, Vidal, Petit Verdot, Viognier, Cabernet Franc, Sauvignon Blanc, and Chambourcin) and four rootstocks (3309, *V. riparia* Gloire, SO4, and 5BB) were represented.

In vineyards, a panel is defined as the space between consecutive wood or metal posts to which the trellis wire is attached, and usually contains 3–5 vines. In each block, the grid (X-distance: 6.06 $\pm$ 0.15 SE m, Y-distance: 7.88 $\pm$ 0.28 SE m) of 80 sample vines consisted of the first vine in the first 10 panels per row in every second row across 16 rows. Before or at the beginning of adult emergence, the area around the base of each sample vine was cleared of vegetation using a "string trimmer" and by raking, leaving a $\approx$1-m-diameter area of clean soil (Johnson et al. 1991). At weekly intervals for 6–8 wk from early July through late August, spanning most of the adult emergence period in Virginia (Pfeiffer et al. 1990, Bergh et al. 2005), pupal exuviae on or protruding from the soil around the base of the vine at each sampling point were collected and recorded.

Nonspatial Measure of Aggregation. Taylor's power law (TPL), a mean-variance-based measure of aggregation, was used to characterize the dispersion of grape root borer pupal exuviae in the blocks. With TPL, the variance (s^2) is related to mean ($\bar{x}$) by a simple power law $s^2 = a\bar{x}^b$, where a and b are parameters representing population characteristics (Taylor 1961). Logarithmic transformations of pupal exuviae variance and mean were used to convert the exponential relationship into a linear relationship, expressed by the regression equation of log variance with log mean, $\log s^2 = b \log \bar{x} + \log a$. The regression coefficient, b is the index of aggregation; an aggregated distribution of counts is indicated when $b > 1$ (Taylor 1961, Taylor et al. 1988). Hypothesis testing of the regression slope (b) equal to 1 was conducted using t-tests ($t =$ [slope – 1]/SE of slope) with ($n - 2$) df at $P < 0.05$ (Davis 1994; Reay-Jones 2010a,b). Regression analysis and the creation of regression plots were carried out in JMP Pro (SAS Institute 2010, Cary, NC).

Spatial Measures of Aggregation. Of the 19 vineyard blocks used in the analysis of TPL, nine blocks were selected to characterize the spatial distribution patterns of grape root borer infestations within each using geostatistical analysis (variograms) and SADIE. The nine blocks were chosen because they each had a mean seasonal pupal exuviae count (ranging from 0.4 to 6.4 per vine) that was greater than the median value of 0.33 exuviae per vine, which was estimated from the 19 blocks.

Geostatistical Analysis. Variography is a geostatistical technique used to assess spatial autocorrelation (or spatial dependence) in a sampled variable through the development of an experimental semivariogram that describes the relationship between sample values with distance and direction within the sampling space. Mathematically, the semivariogram (γ) can be represented by (Cressie 1993, Davis 1994),

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \lfloor z(x_i) - z(x_i + h) \rfloor^2,$$

where $\hat{\gamma}(h)$ is the estimated semivariance for the entity of interest (z) at all points (x_i) separated by lag distance (h), and $N(h)$ is the number of pairs of samples separated by lag distance h.

Removing existing large-scale variation (trend) in the data are a critical step in variography (Isaaks and Srivastava 1989, Cressie 1993, Young and Young 1998). To test for trends in the data, multiple linear regression analysis was used, with pupal exuviae counts as the dependent variable and the spatial references (i.e., X and Y values) of 80 sample points as the independent variables (Park and Tollefson 2006, Karimzadeh et al. 2011) using SAS (PROC REG, SAS Institute 2010). A significant regression ($P < 0.05$) indicated the presence of a trend in the data, which were then subjected to median polishing. The median polishing technique extracts large-scale variation from the data so that the remnant or median polished residuals can be used in variogram analysis to model small-scale variation (Bakhsh et al. 2000, Costa 2009, Frank et al. 2011). The median polished residuals for the pupal exuviae data were derived using code written in MATLAB (MathWorks Inc., Natick, MA) and were then used to develop the semivariograms. Pupal exuviae count data for the vineyard blocks without significant trends were transformed using log ($x + 1$). All of the semivariograms were developed using the geostatistical software GS$^+$ (Gamma Design Software 2008, Plainwell, MI).

The semivariogram has three parameters—range, sill, and nugget—that determine its shape. The range is the physical distance within which data among sample points are spatially correlated or dependent (Liebhold et al. 1993, Fortin and Dale 2005). The semivariance value at which the plotted points level off is the sill, and the nugget is the semivariance value at zero lag distance (Liebhold et al. 1993).

Semivariograms without a sill are fitted either into nugget or linear models, indicating no detectable spatial dependence and a random distribution pattern of the data (Liebhold et al. 1991, Rossi et al. 1992). Semivariograms with a definite sill are fitted either to exponential, spherical, or Gaussian models (Journel and Huijbregts 1978, Isaaks and Srivastava 1989), indicating an aggregated distribution pattern (Schotzko and O'Keeffe 1989, 1990). Both anisotropic (directional) and omnidirectional variograms (Isaaks and Srivastava 1989, Liebhold et al. 1993) were developed for the pupal exuviae data. Anisotropic variograms were calculated at four directions (0, 45, 90, and 135 degrees) with a 22.5 degree offset tolerance. An anisotropy factor (AF), the quotient between minor and major range of anisotropic variograms, was also calculated and used to determine the presence of directional effects in the pupal exuviae count data (Karimzadeh et al. 2011). The best fitted omnidirectional variogram model for the pupal exuviae data in each of the nine blocks was selected based on the smallest value of residual sum of squares (RSS) and the greatest r^2 value (Park and Tollefson 2005, Frank et al. 2011). Evaluation of the degree of aggregation in pupal exuviae counts was based on the nugget-to-sill ratio ($C0/C0 + C$; Trangmar et al. 1986), where <0.25, 0.25–0.75, and >0.75 indicate strong, moderate, and weak aggregation, respectively (Farias et al. 2002, Frank et al. 2011).

Interpolated maps of grape root borer infestations were developed using the geostatistical technique kriging in GS$^+$ (Gamma Design Software 2008). Kriging provides estimates of the variable at unsampled locations based on the weights derived from the variogram model (Isaaks and Srivastava 1989; Liebhold et al. 1991, 1993; Roberts et al. 1993). In particular, ordinary kriging has been used to estimate insect numbers throughout a sampling space (Isaaks and Srivastava 1989, Roberts et al. 1993).

Spatial Analysis by Distance IndicEs. The SADIE method has been used to quantify spatial patterns of insect counts from spatially referenced sample points with x and y coordinates (Perry 1995, Perry et al. 1999). SADIE measures the overall aggregation based on the distance to regularity (D), which represents the minimum total distance that individuals would need to move to achieve the same number (i.e., mean) for each sample point within a sampling area. Higher D values indicate stronger aggregation. The magnitude of D is assessed by a randomization test in which permutations of all observed counts among sample points are performed (Perry and Dixon 2002). The assessment provides an index of aggregation, I_a, with an associated probability, P_a. Aggregated, uniform, and random distribution patterns are indicated by $I_a > 1$, $I_a = 1$, and $I_a < 1$, respectively (Perry 1995). The associated probability (i.e., $P_a < 0.025$ or $P_a > 0.975$) determines whether or not the resultant distribution pattern is significantly different from randomness (Perry 1998).

Estimated and contoured pupal exuviae distribution maps providing a quantitative description of the location, size, and dimension of each cluster were developed by calculating clustering indices for each spatially referenced sample point in SADIE (Perry et al. 1999, Perry and Dixon 2002, Kamdem et al. 2012). Cluster refers to the area of neighboring sampling units with all counts that are either larger or smaller than the sample mean. Clustering indices for each sample point were used to display the clustering area in the form of a patch (i.e., density above average counts) or in a gap (i.e., density below average counts) in a sampling space. Patch cluster refers to areas of strong clustering (cluster indices >1.5) containing counts greater than the overall mean count. Gap cluster is an area with clustering indices <−1.5 caused by relatively fewer counts in neighboring sample points (Perry et al. 1999). Clustering indices representing a patch are denoted by $\bar{\nu}_i$ with associated P value, $P\bar{\nu}_i$, while cluster indices representing a gap are denoted by $\bar{\nu}_j$ with associated P value, $P\bar{\nu}_j$. The presence of significant patches and gaps are indicated by $P\bar{\nu}_i < 0.025$ and $P\bar{\nu}_j < 0.025$, respectively. The calculation of the index of aggregation and index of clustering in SADIE was carried out using SADIEShell (Rothamsted Experimental Station 2008, Herts, The United Kingdom). In total, 1,950 randomizations with a nonparametric option were used for the analysis. Estimated infestation distribution maps containing patches and gaps of the vineyard blocks were developed using the clustering index values (i.e., ν_i and ν_j) of each sample point in JMP (SAS Institute 2010).

Temporal Distribution of Pupal Exuviae. To examine the temporal distribution of pupal exuviae collected during the period of adult emergence, data from 35 of the 48 blocks sampled between 2008 and 2012 were used (n = 9, 7, 3, 8, and 8 blocks in consecutive years from 2008 to 2012, respectively). The blocks were selected based on the following criteria: 1) pupal exuviae were collected weekly for at least 6 wk and 2) the seasonal mean number of exuviae per vine was ≥0.10. Based on the seasonal total number of pupal cases collected per block, weekly mean percentage of total pupal exuviae was calculated.

Predicting Cumulative Pupal Exuviae Counts. Pupal exuviae data from the 35 blocks used for the temporal distribution evaluation were used to calculate mean cumulative counts (weekly) as a percentage of total seasonal counts (Cockfield and Mahr 1994, Milanos and Savopoulou-Soultani 2006, Kamminga et al. 2009). Percentage cumulative pupal exuviae counts across Julian weeks (JWs) during the moth emergence period were fitted to the Weibull function using the following formula (Wagner et al. 1984, Dodson 2006):

$$f(x) = 100(1 - e^{-(x/a)^{\beta}}),$$

where $f(x)$ is the percentage cumulative mean count of pupal exuviae at each JW (x), α is a rate parameter, and β describes the shape of the curve. The fit of the data to the Weibull function was carried out using nonlinear least squares regression in Table Curve 5.01 (SYSTAT Software 2002, Richmond, CA).

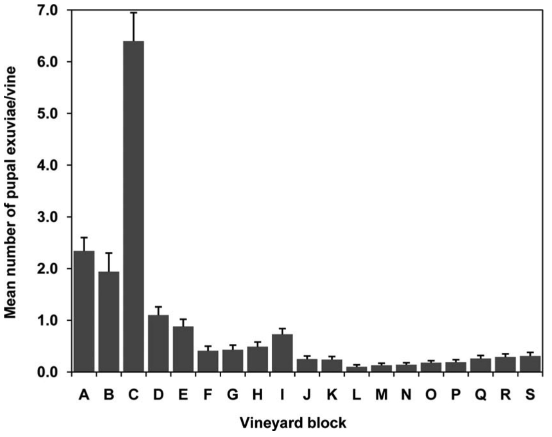

Fig. 1. Seasonal mean (±SE) number of grape root borer pupal exuviae per vine collected from 19 vineyard blocks in Virginia. Blocks A–S used for TPL analysis, and blocks A–I used for geostatistical and SADIE analyses.

Results

Nonspatial Measure of Aggregation. The seasonal mean number of grape root borer pupal exuviae collected per vine varied considerably among the 19 vineyard blocks used for the analysis of TPL (Fig. 1). The analysis showed a significant (t = 28.22; df = 17; P = < 0.001) relationship between logarithmic variance and logarithmic mean of pupal exuviae per vine (Fig. 2). The $r^2 = 0.98$ and $s_e b/b = 0.03$ indicated that the data satisfied the criteria (i.e., $r^2 > 0.8$ and $s_e b/b < 0.2$) for statistical validity (Downing 1986). The slope (b) of the fitted line was also significantly >1 (t = 7.6; df = 17; P = < 0.001), indicating an aggregated dispersion pattern for pupal exuviae within the vineyards (Fig. 2).

Spatial Measures of Aggregation. Grape root borer pupal exuviae were found to be spatially aggregated in vineyard blocks in which mean pupal exuviae densities were ≥0.5 per vine based on the combined results from the variogram and SADIE analyses (Tables 1 and 2).

Geostatistical Analysis. The active lag distance, which is the distance over which the semivariance was calculated, ranged from 34.21 to 44.74 m (Table 1). The uniform lag intervals used ranged from 5.5 to

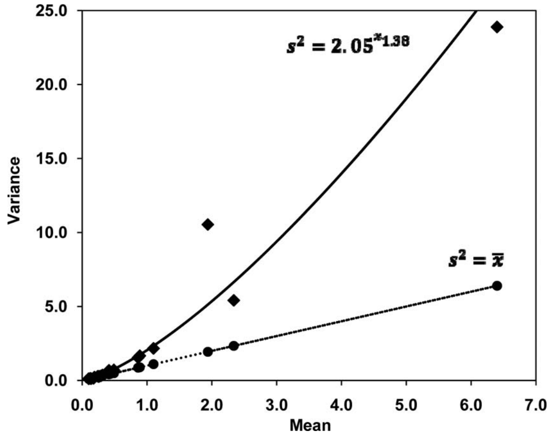

Fig. 2. Fit of grape root borer pupal exuviae counts from 19 vineyard blocks in Virginia to TPL (solid line), indicating aggregation, and a hypothetical fitted equation (dashed line) for variance equal to the mean, indicating random distribution.

6.6 m. None of the nine blocks selected for geostatistical analysis had an anisotropic *AF* value <0.5, suggesting no directional component to pupal exuviae counts. Therefore, only omnidirectional semivariograms were considered further.

Development of omnidirectional semivariograms revealed that five blocks (A, B, C, D, and H) showed an aggregated spatial distribution pattern for pupal exuviae based on the variogram model, model r^2 and RSS, and nugget-to-sill ratio ($C_0/C_0 + C$; Table 1). The r^2 and RSS showed that the best fitted variogram models among the blocks were exponential (block A; r^2 = 0.56), spherical (blocks B, C, D, and H; r^2 = 0.96, 0.73, 0.74, and 0.35, respectively), linear (block E), and nugget (blocks F, G, and I). Because blocks E, F, G, and I produced either a linear or nugget variogram model (Table 1), no evidence of an aggregated distribution was indicated. The nugget-to-sill ratio ($C_0/C_0 + C$), which measures the degree of aggregation, was <0.25 in all blocks in which aggregation was observed, indicating strong aggregation of pupal exuviae (Table 1). Range values for the semivariograms were between 7.24 and 13.58 m, with a mean of 8.8 ± 2.7 SEM (Table 1). Interpolated maps developed by

Table 2. SADIE parameters for grape root borer pupal exuviae distribution in vineyard blocks in Virginia

Block	Mean exuviae per vine[a] (±SE)	I_a	P_a	$\bar{\nu}j$	$\bar{\nu}_i$	$P\bar{\nu}_j$	$P\bar{\nu}_i$
A	2.34 ± 0.26	1.383	0.036	−1.346	1.279	0.048	0.069
B	1.94 ± 0.36	1.393	0.022*	−1.399	1.312	0.025*	0.047
C	6.40 ± 0.55	0.919	0.640	−0.901	0.902	0.730	0.715
D	1.10 ± 0.16	1.014	0.359	−1.024	0.985	0.351	0.441
E	0.88 ± 0.14	2.031	<0.001**	−1.977	1.977	0.001**	0.002**
F	0.41 ± 0.09	0.854	0.862	−0.853	0.848	0.837	0.856
G	0.43 ± 0.09	0.869	0.769	−0.861	0.903	0.794	0.661
H	0.49 ± 0.09	0.912	0.629	−0.917	0.904	0.624	0.660
I	0.73 ± 0.11	1.209	0.099	−1.197	1.158	0.111	0.137

[a] Means were calculated based on the total pupal exuviae counts from each block in one season.

* significant at $P \leq 0.025$, ** significant at $P \leq 0.005$

I_a, index of aggregation; P_a, P value of I_a; $\bar{\nu}_j$, mean value of clustering index over the gap units; $P\bar{\nu}_j$, P value of $\bar{\nu}_j$; $\bar{\nu}_i$, mean value of clustering index over the patch units; $P\bar{\nu}_i$, P value of $\bar{\nu}_i$.

kriging for the blocks in which aggregation was observed are shown in Fig. 3.

Spatial Analysis by Distance IndicEs. The analysis using SADIE also showed spatial aggregation of pupal exuviae in five of the nine blocks analyzed (i.e., A, B, D, E, and I), based on indices of aggregation (I_a) >1 (Table 2). However, spatial aggregation of pupal exuviae was indicated by both SADIE and the geostatistical analysis only in blocks B and D (Table 2). Clustering maps showing patches or gaps were developed using the ν_i and ν_j values for each sample point from blocks A, B, and E (Fig. 4). Visual comparison indicated a high degree of similarity between infestation distribution maps produced using geostatistics (Fig. 3a and b) and SADIE (Fig. 4a and b).

Temporal Distribution of Pupal Exuviae. In 2008, 81% of grape root borer pupal exuviae (n = 9 blocks) were collected between the third week of July (JW 29) and the first week of August (JW 31; Fig. 5a). In 2009 (n = 7 blocks) and 2012 (n = 8 blocks), 82 and 79% of exuviae, respectively, were collected between the second week of July (JW 28) and the first week of August (JW 31; Fig. 5b and d). In 2010, 67% of exuviae (n = 3) were collected between the second and fourth week of July (JWs 28 and 30; Fig. 5c), while in 2011, 77% of exuviae (n = 8) were collected between the

Table 1. Variogram models and parameters for grape root borer pupal exuviae distribution in vineyard blocks in Virginia

Block	Mean exuviae per vine[a] (±SE)	Range (m)	Model	r^2	RSS	Active lag (m)	C_0	C_0+C	C_0/C_0+C	AF
A	2.34 ± 0.26	7.50	Ex	0.56	0.1490	37.65	0.370	3.38	0.109	0.99
B	1.94 ± 0.36	13.58	Sp	0.96	0.0017	34.21	0.045	0.632	0.071	0.99
C	6.40 ± 0.55	7.44	Sp	0.73	0.0003	35.81	0.038	0.43	0.088	0.94
D	1.10 ± 0.16	8.21	Sp	0.74	0.0013	43.42	0.050	0.382	0.131	0.99
E	0.88 ± 0.14	–	Li	0.02	0.0270	43.42	0.965	0.997	0.968	–
F	0.41 ± 0.09	–	Nu	0.80	0.0020	35.81	0.198	0.198	1.000	–
G	0.43 ± 0.09	–	Nu	0.64	0.0028	43.42	0.172	0.172	1.000	–
H	0.49 ± 0.09	7.24	Sp	0.35	0.0024	44.74	0.038	0.203	0.188	1.0
I	0.73 ± 0.11	–	Nu	0.47	0.0006	35.81	0.272	0.272	1.000	–

[a] Means were calculated based on the total pupal exuviae counts from each block in one season.

RSS, residual sum of squares; C_0, nugget; C_0+C, sill; C_0/C_0+C, nugget-to-sill ratio; AF, anisotropy factor; Nu, nugget model (C_0 = C_0+C); Ex, exponential model; Sp, spherical model; Li, linear model.

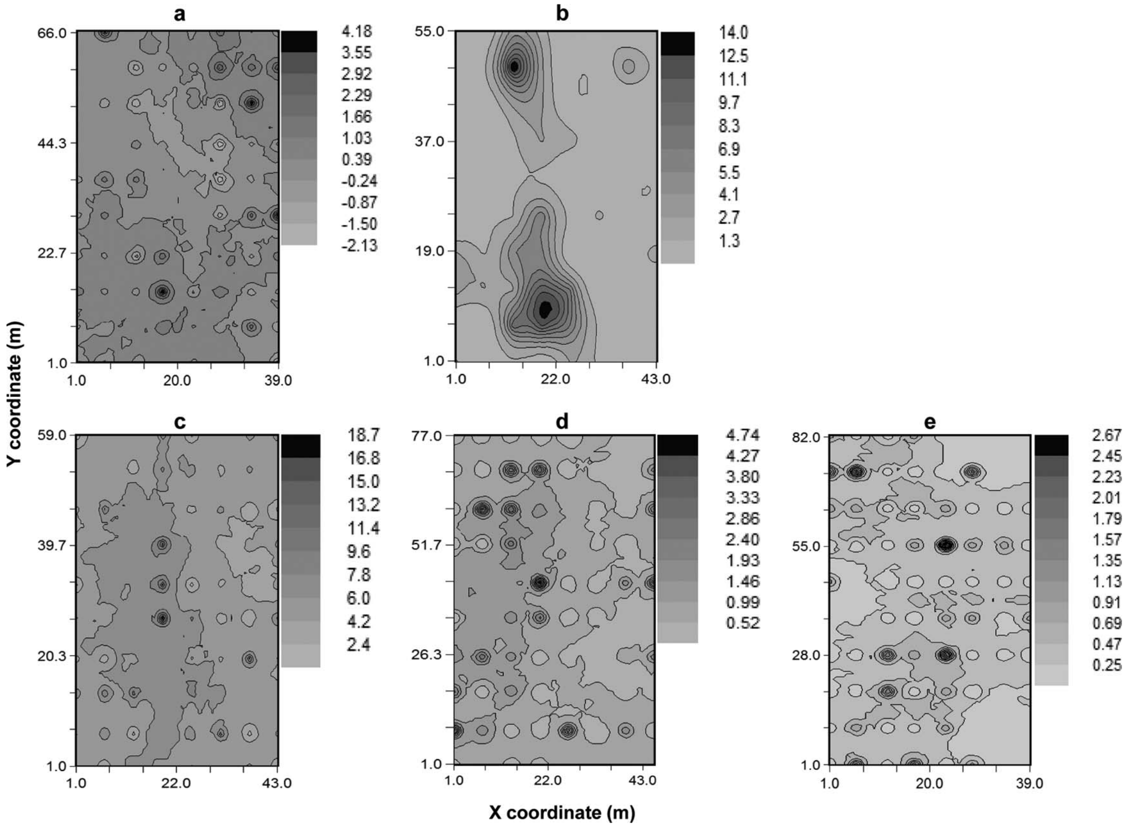

Fig. 3. Interpolated maps, developed using kriging based on the asymptotic variogram models, of grape root borer pupal exuviae distributions in five vineyard blocks in Virginia. (a, b, c, d, and e) represent vineyard blocks A, B, C, D, and H from Fig. 1, respectively

fourth week of July (JW 30) and the second week of August, (JW 32; Fig. 5e).

Predicting Cumulative Pupal Exuviae Counts. The fit of percentage cumulative mean count of pupal exuviae to the Weibull function was significant (F = 1710.08; df = 1, 6; P = < 0.0001; r^2 = 0.995; Fig. 6), with α = 30.28 ± 0.06 SE and β = 20.25 ± 1.07 SE. Based on the Weibull model, 34% of total seasonal exuviae were collected by the third week of July (JW 29), 56% by the fourth week of July (JW 30), 80% by the first week of August (JW 31), and 95% by the second week of August (JW 32). In predicting the peak moth emergence period using the Weibull function, 80% of total seasonal exuviae were collected between JWs 27 and 31, 70.7% during JWs 28–31, and 61.5% during JWs 29–31.

Discussion

Characterization of the spatial distribution of grape root borer pupal exuviae within commercial vineyard blocks has improved the ability to monitor infestations of this important and insidious below-ground pest, and by extension, should assist future research efforts and enable more informed management decisions by growers. Although a nonspatial technique indicated that grape root borer pupal exuviae showed an aggregated dispersion pattern within the vineyard blocks, the use of geostatistical analysis and SADIE showed true spatial aggregation only in blocks with ≥0.5 exuviae per vine. Based on the extent of spatial dependency indicated by the range value of the variogram model, counts of pupal exuviae appeared to be aggregated within a mean distance of 8.8 m.

Both exogenous and endogenous factors can influence insect distributions and contribute to aggregated distribution patterns. Exogenous factors such as climate, soil type, topography, stochastic disturbances, and solar activities may contribute to large-scale variation by creating microenvironments favoring aggregation (Ellsbury et al. 1998, Toepfer et al. 2007).

Endogenous influences include biological (e.g., host-finding and oviposition behavior) and ecological factors (e.g., predation or parasitization risks) characteristic of individual species (Dormann 2007). Spatial distribution patterns of immature insects can also be influenced by adult distributions during their period of peak emergence (Toepfer et al. 2007). For example, both adult and larval cutworms, *Agriotes sordidus* Illiger and *Agriotes litigiosus* Rossi, were found to be spatially clustered based on separate experiments conducted in two different cropping systems

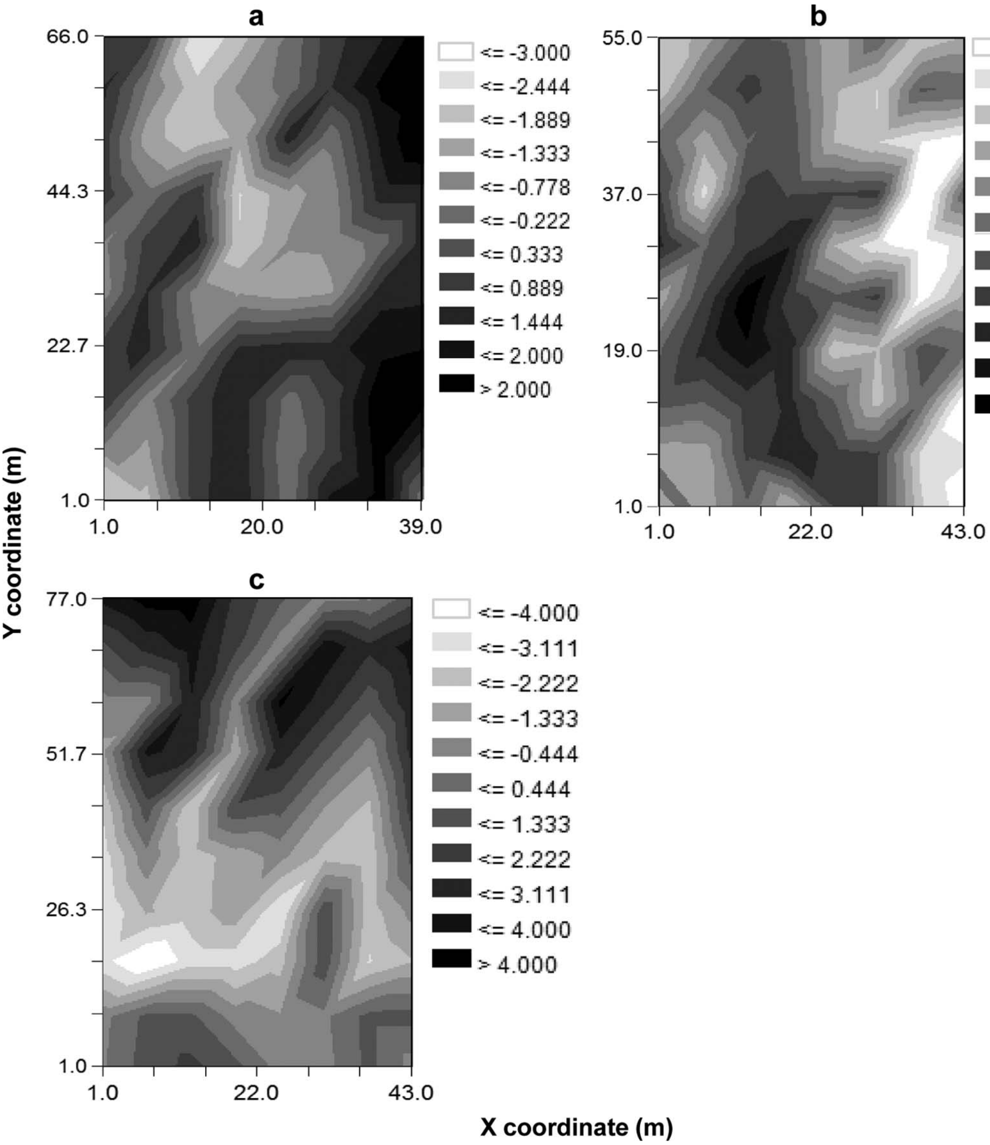

Fig. 4. Estimated maps of grape root borer pupal exuviae distribution using clustering index values (i.e., v_i and v_j) of each of 80 sample points. (a, b, and c) represent vineyard blocks A, B, and E from Fig. 1, respectively. Sampled areas having all sample points with cluster indices >1.5 and <−1.5 are referred to as "patches" and "'gaps," respectively.

(i.e., a mixed cropping system of organic vegetable and fruit crops and a cereal cropping system) in northern Italy (Furlan and Burgio 1999, Burgio et al. 2005). Grape root borer larvae are thought to have a 2-yr developmental period in Virginia, thus the abundance and distribution of pupal exuviae measured in an individual vineyard block in any given year would have been influenced primarily by adult emergence and oviposition, and larval establishment on roots, 2 yr previously. Upon emergence, adult female grape root borer typically rest on the lower trunk of a vine near the emergence site, and eventually walk up into the canopy (Pearson 1992) where calling and mating occur (Dutcher and All 1978a). Females carrying a full egg complement exhibit rather sluggish flight, and as is often the case with other moths (Bernays and Chapman 1994), theymay at least initially oviposit in the vicinity of the emergence and mating site, where larval resources in this perennial plant are often spatially and temporally stable (Greenfield 1981). Although the distance over which ovipositing female grape root borers move has not been quantified, Brooks (1907) observed a female depositing single eggs at intervals of a few inches over a distance of ≈3 m along a vine cordon. Limited flight distance of ovipositing females could also reduce the risk from predation by natural enemies (Greenfield 1981), including insectivorous birds such as the barn swallow (*Hirundo rustica eryth-*

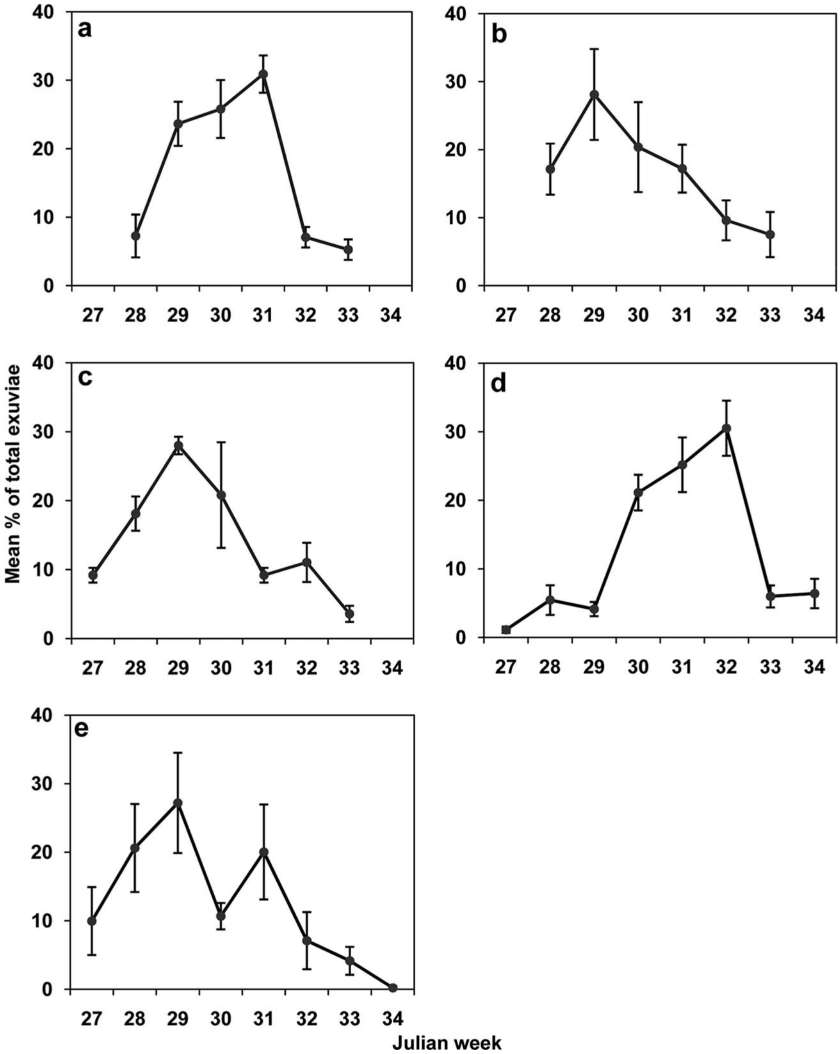

Fig. 5. Mean (±SE) weekly percentage of total grape root borer pupal exuviae collected from vineyard blocks in Virginia in (a) 2008, (b) 2009, (c) 2010, (d) 2011, and (e) 2012. In consecutive years between 2008 and 2012, 9, 7, 3, 8, and 8 blocks were sampled, respectively. JWs 28 and 32, represent 9–15 July and 6–12 August, respectively.

rogaster Boddaert), mocking bird (*Mimus polglottos polyglottos* L.), and great crested fly catcher (*Myiarchus crinitus* L.), that are known to attack it in vineyards (Brooks 1907, Clark and Enns 1964).

Unlike the contribution of nearby wild *Vitis* to higher infestations of grape berry moth, *Paralobesia viteana* (Clemens), in vineyard border rows (Hoffman and Dennehy 1989), interpolated pupal exuviae distribution maps from these vineyard blocks showed no evidence of higher densities at or near the edges (Fig. 3). Of the nine blocks used in the spatial analysis, four blocks had at least one edge in close proximity (≤65 m) to a wooded area from which grape root borer infestations in commercial plantings are thought to originate (Snow et al. 1991, Bergh 2006), although the presence and abundance of wild *Vitis* in those areas was not assessed.

Spatial distribution is a complicated and multidimensional phenomenon and the use of more than one analytical approach, including traditional and spatial techniques, has been recommended for better clarity and interpretation of results (Madden and Hughes 1995, Perry et al. 2002). The suitability of different methods for spatial data analysis and their interpolation techniques were reviewed by Legendre and Fortin (1989). Although differing results from such uses of traditional and spatial techniques to determine aggregations of several insect species have been reported (Young and Young 1990, Midgarden et al. 1993, Fortin and Dale 2005), results from one method should not negate those from others because different approaches elucidate different aspects of insect distribution patterns, and together provide better accuracy (Perry et al. 2002, Queiroz et al. 2010). Although

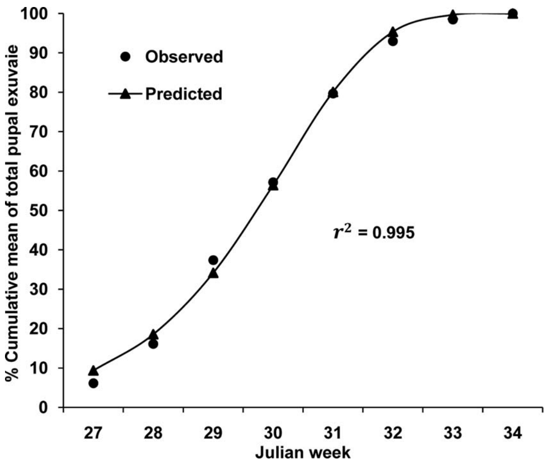

Fig. 6. Percentage cumulative mean grape root borer pupal exuviae from pooled data (2008–2012) collected from 35 vineyard blocks in Virginia (solid circle) fitted to the Weibull function (solid line with solid triangle), $f(x) = 100(1 - e^{-(x/\alpha)^{\beta}})$. In the Weibull function, $\alpha = 30.28 \pm 0.06$ SE and $\beta = 20.25 \pm 1.07$ SE.

traditional measures of aggregation such as TPL have been widely used to determine insect dispersion and distribution, they do not represent true spatial distribution patterns. In this study, TPL showed a strong aggregation of grape root borer pupal exuviae in vineyards, while variogram analyses provided additional information on the spatial autocorrelation or spatial dependence of pupal exuviae with distance and direction within the vineyard blocks (Fortin and Dale 2005). The variograms and their parameters indicated a strongly aggregated distribution of grape root borer pupal exuviae in 5 of 9 vineyard blocks. Wright et al. (2002) reported that feeding injury from larval European corn borer, *Ostrinia nubilalis* (Hübner), showed an aggregated distribution pattern at 4 of 7 sites. Farias et al. (2003) showed that the distribution of three sharpshooter species trapped in yellow sticky cards over several seasons in a citrus orchard resulted in fitted variograms for 9 of 36 datasets. Similarly, the distribution of plant pathogenic nematodes in cotton showed an aggregated distribution in some but not all fields (Farias et al. 2002). Of the nine blocks included in the geospatial analysis, seven blocks (A, B, C, D, E, H, and I) showed evidence of aggregation of pupal exuviae based on the combined results from the variogram and SADIE analyses. The different results from the two types of spatial analyses could possibly be due to the different ways by which spatial weights for individual sample points are calculated (Kamdem et al. 2012). Our use of SADIE indicated an aggregated pupal exuviae distribution pattern in five of the nine vineyard blocks, although only two showed statistically significant aggregation. Because SADIE measures true clustering among neighboring sample points, isolated higher values from individual sample points do not contribute to aggregation. Variogram analyses, however, incorporate these higher values in the analysis and are more appropriate for characterizing and estimating the local population abundance and density (Perry et al. 2002, Perry and Dixon 2002). Other studies in which both geostatistical analyses and SADIE were used to quantify spatial distributions of insects yielded variations similar to those reported here (Perry et al. 2002, Karimzadeh et al. 2011, Kamdem et al. 2012).

Our results showed that grape root borer pupal exuviae tended to be spatially aggregated in vineyard blocks in which pupal exuviae densities were ≥0.5 per vine. Similar density-dependent aggregation patterns have been reported for western corn rootworm, *Diabrotica virgifera virgifera* LeConte, and grass thrips, *Anaphothrips obscurus* (Müller) (Midgarden et al. 1993, Reisig et al. 2011). Aggregation is usually not detected from sampled areas with a low density of the variable of interest (Taylor et al. 1978, Taylor 1984, Lepš 1993, Blom and Fleischer 2001), as variance and mean are often equal, rendering spatial distributions indistinguishable from random (Chiang and Hodson 1959, Taylor et al. 1978). In blocks F and G, which showed no evidence of aggregation from either variogram or SADIE analyses, at least 70% of the sampled vines yielded no pupal exuviae, likely contributing to our inability to detect an aggregated distribution in those blocks.

Understanding the spatial distribution of an insect species is a key component for developing a quantitative and efficient sampling scheme (Legendre and Fortin 1989, Fortin and Dale 2005, Park and Tollefson 2006). Sampling schemes developed for other pest insects that were based on spatial distributions used an appropriate sampling method (systematic, random, or stratified) in a gridded (square, triangular, or hexagonal) sampling space (Schotzko and O'Keeffe 1990, Williams et al. 1992, Liebhold et al. 1993, Wright et al. 2002, Frank et al. 2011). Sampling distance can differ according to the intended purpose. If the intention is to develop infestation density maps for site-specific management (Fleischer et al. 1999), as has been used for some agricultural pests (Weisz et al. 1996, Blom et al. 2002), sampling should be within the distance of the range value of the variogram (8.8 m for grape root borer exuviae; Weisz et al. 1995, Park and Tollefson 2005, Frank et al. 2011). However, there are several reasons why a map-based precision approach for grape root borer management may not be a pragmatic option for growers. First, collecting the data to develop prediction maps for this pest over large vineyard acreage would be very labor-intensive. Second, map development requires specialized software and expertise that is relatively uncommon and not readily accessible to many growers. Finally, there are only two registered products considered effective for grape root borer management: 1) chlorpyrifos applied as a soil drench around the vine base as a barrier to neonate movement to roots, and 2) mating disruption using Isomate-GRB. Most growers are averse to chlorpyrifos applications unless infestations have reached critical levels (Bergh 2012), and mating disruption requires treatment of entire vineyards or vineyard blocks. Consequently, sampling grape root borer pupal exuviae to quantify its relative abundance or to evaluate the effectiveness of control measures appear to be the best uses of this monitoring approach. For these purposes, use of a sampling distance that is higher than the range value of the variogram is necessary to obtain independent samples.

Regardless of the intended use of data from grape root borer pupal exuviae sampling, accurate assessment of its presence and abundance requires removal of all living and dead vegetation around the base of sample vines in early July. We recommend a cleaned area around each sample vine of ≈1 m diameter, as Dutcher and All (1978c) showed that ≈90% of grape root borer pupal exuviae were recovered from a circular area of ≈35-cm radius around the vine base. This can be accomplished easily with herbicide or a "string trimmer" and raking, typically involving only a few minutes per vine. We also recommend weekly visits to all sample vines during the assessment period because exuviae that are left on the soil surface are prone to being displaced by storms, mowers, or airblast sprayers. Exuviae left protruding from the soil surface are not as prone to being dislodged (J.C.B., unpublished data).

Our sampling from 2008 to 2012 revealed that, on average, 63.2% of all pupal exuviae were found between the third week of July and the first week of August, and 73.6% were found between the second week of July and the first week of August. Based on pupal exuviae counts from three vineyards in two consecutive years in North Carolina, Pearson (1992) found that the peak emergence of adult grape root borer ranged from the first to the last week of August, and that the duration of adult emergence was somewhat longer than reported here. Similar latitude-dependent differences in the seasonal patterns of adult grape root borer emergence were reported by Brooks (1918) and Snow et al. (1991). Air temperature and rainfall are two factors that likely influence the onset, peak, and duration of grape root borer emergence (Clark and Enn 1964, Sarai 1972). The average daily temperature from June through August in the consecutive years from 2008 through 2012 recorded at Virginia Tech's Alson H. Smith, Jr. Agricultural Research and Extension Center, Winchester, VA, was 22.1, 21.8, 24.3, 23.7, and 22.7 °C, and average daily rainfall was 3.4, 2.5, 1.6, 1.7, 3.4 mm, respectively. The unusually hot and dry conditions in Virginia that prevailed during late spring and summer in 2010 may explain the earlier onset and peak of grape root borer emergence than was recorded in other years. Although peak emergence of adult grape root borer may occur ≈1 wk earlier in such years, weekly sampling throughout the 3- or 4-wk periods mentioned above should provide a reasonable estimation of its abundance in most seasons, with least effort. Nowatzki et al. (2002) noted that scouting during the period of peak adult emergence of northern and western corn rootworm, *Diabrotica barberi* Smith & Lawrence and *D. virgifera virgifera*, was efficient for assessing infestations. Importantly, our recommended sampling period for grape root borer pupal exuviae coincides with a period during which labor required for other tasks in mid-Atlantic vineyards is much reduced (T. K. Wolf, personal communication). In other eastern states where grape root borer is an economic pest, the appropriate sampling period may differ somewhat from that reported here because of different seasonal patterns of moth emergence (Snow et al. 1991, Pearson 1992).

By coupling the results of our analyses of the spatial distribution of grape root borer infestations with its seasonal patterns of emergence in Virginia vineyards, we recommend a systematic sampling scheme for this pest that involves weekly pupal exuviae collections between mid-July and early August from a grid of sample vines in blocks to be assessed. The strong fit of the cumulative percentage of emergence from pooled data across all years to the Weibull function should enable growers or researchers to accurately capture specific ranges of percentage emergence, according to individual needs. Variogram analyses indicated an appropriate inter-vine sampling distance of ≈9 m to achieve independent samples for population density assessment. Based on vine spacing that is typical for vineyards in Virginia, a sample vine spacing of 9 m is equivalent to one vine per 1.5 panels along the row. We recommend a grid of sample vines constituted of vines in every second row and of a minimum of 50 vines per vineyard block of average size (≈1–2 ha). With relatively little training and experience, one person could survey 50 vines in ≈30 min. All pupal exuviae found must be removed to avoid recounting during subsequent surveys.

Dutcher and All (1979b) calculated an economic threshold of 0.074 larvae per vine for grape root borer feeding on roots of 'Concord' vines (*Vitis labrusca* L.) in Georgia and recommended intervention upon detection of the pest. Because 38 of the 48 blocks surveyed in Virginia between 2008 and 2012 exceeded this recommended threshold (J.P.R., unpublished data), based on total numbers of pupal exuviae collected per vine, but most showed no apparent effects from the pest, Bergh (2012) suggested that the threshold recommendation by Dutcher and All (1979b) may be conservative for grape root borer on *V. vinifera* in the mid-Atlantic region. Although the development of economic thresholds for grape root borer on *V. vinifera* in Virginia and surrounding states would add importantly to the utility and interpretation of sampling data, in the interim the sampling scheme we propose should greatly improve the ability to assess and manage grape root borer infestations in vineyard blocks.

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