Effects of Biotic and Abiotic Factors on Grape Root Borer (Lepidoptera: Sesiidae) Infestations in Commercial Vineyards in Virginia

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ABSTRACT Larval grape root borer, *Vitacea polistiformis* (Harris) (Lepidoptera: Sesiidae), feed on roots of wild *Vitis* and commercially important *Vitis* species and rootstocks in portions of the eastern United States. Grape root borer pupal exuviae sampling in Virginia vineyards from 2008 to 2012 revealed that infestation levels varied substantially among 48 vineyard blocks. Data on horticultural (cultivar, rootstock, vine age, and planting area), cultural (insecticide use, ground cover, weed control, and irrigation), and environmental variables (proximity to forest, soil composition, soil moisture holding capacity, pH, organic matter, bulk density, and cation exchange capacity) from each block were subjected to optimal quantification using categorical principal component analysis (CATPCA). Variables with component loading values ≥0.70 from the CATPCA were used as predictors and pupal exuviae density as the dependent variable in binary logistic regression. A prediction model was developed by including statistically significant variables in the logistic regression. CATPCA showed that seven vineyard factors (ground cover, soil texture, soil mass moisture, soil pH, clay/sand ratio, clay/silt ratio, and sand/silt ratio) based on three selected principal components were significant for subsequent regression analysis. Binary logistic regression showed that soil mass moisture and clay/sand ratio were statistically significant factors contributing to differences in infestation among vineyard blocks. Based on these two factors, a risk prediction model for calculating the probability of grape root borer infestation in vineyards was developed and validated using receiver operating characteristic curve. Results are discussed in relation to the practical implications of a predictive, risk assessment model for grape root borer management.

KEY WORDS *Vitacea polistiformis*, *Vitis vinifera*, risk factor, CATPCA, logistic regression

Many biotic and abiotic factors can influence the establishment and density of belowground insect herbivores on the roots of cultivated host plants (Brown and Gange 1990, Erb and Lu 2013). Horticultural factors may include cultivar (Shapiro and Gottwald 1995), rootstock (Beavers and Hutchison 1985, Du et al. 2009), plant age (Alinia et al. 2000), or crop acreage (Nagoshi 2009). Cultural factors related to crop management, such as insecticides, irrigation, ground cover, or weed control can also influence pest density and extent of crop damage (Godfrey and Yeargan 1985, Townsend 1991, Tonhasca and Stinner 1991, Oyediran et al. 2007). Environmental variables that may affect populations of belowground pests include the presence and proximity of wild hosts (Hoffman and Dennehy 1989), weather and associated effects on soil properties (Sarai 1972, Brown and Gange 1990), and natural enemies (Williams et al. 2010, Shapiro-Ilan et al. 2003). Soil properties that may be important to the survivorship of belowground insects include soil moisture (Johnson et al. 2010), texture (Brown and Gange1990, Brust and House 1990), particle size (Lummus et al. 1983), pH (Li et al. 2007, Johnson et al. 2010), and organic matter content (Brust and House 1990, Villani and Wright 1990). Species that show a Type-III survivorship curve characterized by high mortality during the egg and early larval stages (Hawley 1949, Marrone and Stinner 1983), such as the grape root borer, *Vitacea polistiformis* (Harris) (Lepidoptera: Sesiidae) (Dutcher and All 1978), may be particularly vulnerable to the effects of these soil properties. In addition, soil characteristics can affect the mobility of belowground species (Strnad and Bergman 1987, Gustin and Schumacher 1989, Pacchioli and Hower 2004) and the diffusion of behaviorally active compounds from host roots (Villani and Wright 1990, Johnson and Gregory 2006).

Grape root borer has been considered a pest of grapevines in parts of the eastern United States for

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>150 yr (Harris 1854, Walsh 1868, Clark and Enns 1964, Pollet 1975, Dutcher and All 1976, Bergh 2012). The oligophagous larvae feed on roots of plants in the family Vitaceae, including wild *Vitis* species and commercially important *Vitis* species and rootstocks. Larval feeding creates large channels packed with reddish frass in the root cortex (Dutcher and All 1979a, Bergh 2012). A severe infestation by grape root borer can result in discolored and smaller leaves, reduced shoot growth, fewer and smaller berries, and vine wilting (Sorensen 1975, All et al. 1987). All et al. (1987) reported that vines usually begin to show symptoms after 5–10 yr of infestation and these vines decline over the subsequent 3- to 5-yr period. In severe cases, the cumulative effects of infestations may lead to vine death (Dutcher and All 1976). Importantly, diagnosing a grape root borer infestation based on symptoms expressed by the aboveground parts of vines is hindered by the fact that these symptoms, known collectively as "slow vine decline" (All et al. 1987), also can be caused by a number of other horticultural and pathological conditions.

Compared with many sesiid species, which deposit eggs on specific host parts (Gentry and Wells 1982, Koehler et al. 1983, Leskey and Bergh 2005), female grape root borers oviposit indiscriminately on aboveground parts of vines and on nearby vegetation (Brooks 1907, Sorensen 1975, Dutcher and All 1979a) from July through August in Virginia. Newly hatched neonates enter the soil to find and establish on grape roots and vine infestation is ultimately dependent upon their success during this critical phase. In Virginia, larvae feed for ≈2 yr before pupating beneath the soil surface around the base of vines on which they developed (Clark and Enns 1964, Dutcher and All 1979a), and infested vines may support overlapping generations. On emerging from the soil, adult grape root borers leave a relatively large, copper-colored pupal exuviae protruding from or lying on the soil. Sampling pupal exuviae at regular intervals through the period of adult emergence is the only nondestructive and most accurate and unequivocal method by which to assess the presence of larvae on individual vines (Bergh 2012).

Anecdotal reports from Virginia and neighboring states have indicated that the extent of vineyard infestation by grape root borer can vary tremendously; some sites become heavily infested and suffer significant impacts, while others are relatively unaffected. A long-standing and serious issue with grape root borer is that growers are often unaware that an infestation has developed until the effects on vine health and productivity have become apparent (Brooks 1907, Dutcher and All 1979b). Despite these circumstances, the factors underlying differences in grape root borer density among vineyards and vineyard blocks have not been examined comprehensively or holistically.

The individual effects of some of the biotic and abiotic variables on the survival of grape root borer neonates have been examined in laboratory or field studies. Although rootstocks containing the Florida leatherleaf grape, *Vitis shuttleworthii* House, in their parentage showed some level of resistance to larval establishment (Webb and Mortensen 1990), the general consensus is that most commercially important rootstocks and cultivars are susceptible to this pest (Massey 1945, Wylie 1972, Wylie and Johnson 1978, Webb and Mortensen 1990, Harris et al. 1994). Bergh et al. (2011) showed that neonate grape root borers responded positively to ethanol-based extracts of roots from several native *Vitis* species and commercial rootstocks, with indications of a stronger response to some. Subsequently, Rijal et al. (2013) found that volatile emissions from roots were attractive to larvae. Although Harris et al. (1994) noted higher levels of grape root borer infestations on older vines, All et al. (1987) reported that 1-yr-old vines were infested and we have observed numerous instances of 3- to 5-yr-old vines supporting larval populations. Townsend (1991) evaluated the effects of various cover crop and irrigation regimens on grape root borer pupal exuviae densities and found no significant influence of those factors. The effects of rainfall and soil moisture on the mortality of larval grape root borer also have been reported (Clark and Enns 1964, Sarai 1972).

Despite previous evaluations of the influence of some vineyard factors on grape root borer populations, much remains unknown about the individual or combined effects of the many variables that may influence this pest under field conditions. Identifying potential risk factors that may underlie vineyard vulnerability to grape root borer and associated differences in population densities among sites should provide important information toward understanding the relative risk from this insidious pest for individual vineyards or vineyard blocks. Here, we report the results of a multiyear study comparing data from intensive pupal exuviae sampling in 48 vineyard blocks in Virginia with measurements of a broad range of biotic and abiotic variables taken from the sample sites.

Materials and Methods

Site Selection and Preparation. For the purposes of this study, a vineyard was defined as the total area planted with grape on each farm, regardless of cultivar or rootstock. A vineyard block, therefore, was a portion of a vineyard within which the vines were essentially uniform in cultivar, rootstock, vine age, and other environmental and cultural practices. The vineyard blocks at our study sites were 1.42 ± 0.45 SE ha, and within each block, an area of ≈0.4 ha was designated for sampling grape root borer pupal exuviae. Forty-eight blocks from 19 commercial vineyards (2 or 3 blocks per vineyard) in northern and central Virginia were used for sampling and were located in Loudoun ($n = 11$), Rappahannock ($n = 8$), Shenandoah ($n = 5$), Rockingham ($n = 3$), Albemarle ($n = 11$), Fauquier ($n = 3$), Frederick ($n = 4$), and Nelson ($n = 3$) counties. Forty-four blocks were sampled once between 2008 and 2012. In 4 of the 48 blocks, the same vines were sampled in each of the 3–4 consecutive years; however, for those 4 blocks, only the pupal exuviae data collected during the first year of sampling were used in categorical principal component analysis (CATPCA) and regression analyses. None of the blocks selected were treated with an insecticide targeting grape root borer (i.e., chlorpyrifos) or with grape root borer mating disruption before or during the study.

Over the five years of the study, we selected blocks that represented a range of the cultural, horticultural, and environmental variables of interest. Sampled blocks contained vines that were 2- to 23-yr-old (mean = 11.5 ± 0.8 SE). The 11 grape cultivars represented included Chardonnay ($n = 7$), Vidal ($n = 7$), Petit Verdot ($n = 5$), Viognier ($n = 5$), Cabernet Franc ($n = 8$), Riesling ($n = 1$), Merlot ($n = 2$), Norton ($n = 3$), Cabernet Sauvignon ($n = 5$), Sauvignon Blanc ($n = 1$), and Chambourcin ($n = 4$). The seven rootstocks represented were 3309 ($n = 24$), 101-14 ($n = 4$), *Vitis riparia* Gloire ($n = 4$), SO4 ($n = 8$), 5BB ($n = 3$), own-rooted Norton ($n = 3$), and own-rooted Vidal ($n = 2$). The blocks varied in their proximity to forested areas, but neither the presence nor abundance of wild *Vitis* at the border or interior of those areas was quantified.

As per standard viticulture terminology, a panel was defined as the space between consecutive posts to which the trellis wire was attached, and typically contained 3–5 vines. Most sampling areas ($n = 30$) consisted of a rectangular grid of 80 sample vines that included the first vine in each of the 10 consecutive panels within a row, in every second vine row across 16 rows. In the remaining vineyard blocks ($n = 18$), the sampling area consisted of a grid of 39−118 sample vines. The sampling areas were prepared for the survey in late June or early July of each year. All vegetation and debris were removed to create a clean soil surface within a ≈1-m-diameter circle around the trunk of each sample vine. In blocks with weeds or grass in the vine rows, the vegetation was removed using a "string trimmer," followed by raking, while only raking was required in blocks with cleaner cultivation in the rows. During the sampling period, weeds that began to grow in the cleaned area were removed by hand during the weekly visits to every vine.

Pupal Exuviae Sampling and Measurement of Vineyard Variables. At weekly intervals between early July and late August, the clean area around the base of each sample vine was inspected. The number of grape root borer pupal exuviae found was recorded and all exuviae were removed from the site.

The cooperating growers provided horticultural information about the cultivar, rootstock, vine age, and planting area for each vineyard block sampled. Information on cultural and pest management practices including insecticide use, ground cover and weed control, and irrigation was obtained via a questionnaire to the manager of each vineyard. As grape root borer has a 2-yr developmental period in Virginia, the pupal exuviae sampled in any given year represented the generation that was initiated 2 yr previously. The questionnaire was designed to capture information about the practices that occurred 2 yr before the year in which pupal exuviae were sampled, focusing on the period between late June and early September when grape root borer adults are active and larvae are hatching from eggs. Insecticide use included the name, rate, and frequency of insecticide applications. Information on the percentage of ground cover, including weeds and grass in the vine rows, was based on a rating system of 1 (1–40% cover) and 2 (>40% cover). Data on weed control were based on a qualitative scale that rated the intensity of weed control practices used by growers, where 1 = none, 2 = light, 3 = medium, and 4 = aggressive control. Information about the use of irrigation was based on a binary, yes or no response.

Because native species of *Vitis* in unmanaged woodlots and forests adjacent to vineyards are considered the initial source of grape root borer in new plantings (Snow et al. 1991, Bergh 2006), and thus could influence pest density, the distance from the edge of each block sampled to the nearest forested area was measured using the "add path" and "ruler" functions in Google Earth (Google Inc. 2013, Mountain View, CA). At equally spaced intervals, five parallel distances between the edge of each vineyard block and the nearest woodland were measured and averaged.

In October and November 2012, a 25-cm-long soil core sample was taken from each corner and the center of each sampled area (≈0.4 ha) using a standard soil auger. The five soil samples from each vineyard were combined to create one composite sample for each area, following standard protocols (Donohue 2000). Analysis of the samples for soil organic matter, pH, texture, particle size analysis, soil mass moisture, and cation exchange capacity was conducted at the Virginia Tech Soil Testing Laboratory, Blacksburg, VA. Percent soil mass moisture was estimated based on the water holding capacity of soil. The soil samples were saturated with water and were subjected to an atmospheric pressure of 33,333 Pa (i.e., one-third bar), which forces water out of the soil sample. The final soil mass moisture was calculated as the percentage of weight difference between wet soil at 33,333 Pa pressure and oven-dried soil (i.e., at 105°C). In addition, one sample using a core ring sampler (5.08 cm in diameter and length) was collected from each block, oven-dried at 105°C for 24 h, and weighed. The bulk density of each sample was calculated.

Statistical Analyses. Nonlinear principal component analysis, also known as CATPCA, can be used instead of traditional PCA to explore nonlinear relationships in cases for which the data are comprised of both qualitative (i.e., nominal and ordinal variables) and quantitative variables (Linting and van der Kooij 2012). The two main purposes for using CATPCA are to reduce the dimensionality of original variables to a few uncorrelated principal components (PCs) and to remove the likelihood of multicollinearity among variables for statistical validity (Howling et al. 1993, Graham 2003). Initially, the 18 biotic and abiotic variables described above were subjected to a nonlinear optimal quantification process, called optimal scaling, which transformed the qualitative variables into quantitative variables (Linting et al. 2007). Data on grape cultivar, rootstock, and soil texture (nominal variables), ground cover, weed control, and irrigation (ordinal variables), and vine age, planting area, proximity to forest, number of insecticide sprays, soil pH, soil bulk density, soil organic matter, soil cation exchange capacity, soil mass moisture, clay/sand ratio, clay/silt ratio, and sand/silt ratio (numeric variables) measurements were included in the CATPCA analysis, conducted using SPSS (IBM Corp. 2012, Armonk, NY). The stepwise process of CATPCA was as described below.

Analysis Level Selection and Discretization. Analysis level selection refers to the amount of freedom allowed in transforming categorical values (i.e., labels) to category quantifications. Nominal scaling, spline ordinal scaling, and numeric scaling were used for the quantification process of nominal, ordinal, and numeric variables, respectively, from each sampled block. Following this was a discretization step by which continuous or zero values were converted to integers to satisfy the computational requirement of CATPCA (Linting and van der Kooij 2012). All nominal and ordinal variables were discretized using the "ranking" option, while numeric variables were discretized using the "multiplying" option. With CATPCA, only cells with missing values were excluded from the analysis, rather than excluding entire rows or columns with missing values, as is the case with the traditional linear PCA. In 12 of the 48 vineyard blocks, there were one or more variables with missing values.

PCs and Variable Selection. We selected three PCs using two criteria: the total variance explained by the selected PCs (Comrey 1973, Linting and van der Kooij 2012) and the scree plot (Fabrigar et al. 1999).

The internal consistency (i.e., the degree of relatedness among variables) was assessed by Cronbach's Alpha, in which a value of ≥ 0.70 indicated strong internal consistency among variables (Cortina 1993). Original variables that had component loadings of ≥ 0.70 across the selected PCs, as indicated by CATPCA, were selected to determine the association of the vineyard variables with grape root borer pupal exuviae densities (i.e., mean total number of pupal exuviae per vine).

Binary logistic regression analysis was conducted, using a measure of infestation status (see below) as the dependent, indicator variable, and the selected vineyard variables from the CATPCA as predictors. Although Dutcher and All (1979b) reported an economic threshold of 0.074 larvae per vine based on a study in Concord grape, *Vitis labrusca* L. in Georgia, Bergh (2012) suggested that this may be very conservative for grape root borer on *Vitis vinifera* L. in Virginia. Therefore, we used a cut-off of 0.10 pupal exuviae per vine to separate the sampled areas into two infestation status categories for binary logistic regression analysis: lightly infested (≤ 0.10 exuviae per vine; $n = 17$) and heavily infested (>0.10 exuviae per vine, $n = 31$). These categories were indicated by 0 and 1, respectively, in the logistic regression analysis.

The statistical significance of the regression model was tested using the omnibus test statistic (Maroof 2012), and the fit of the model was measured by Nagelkerke r^2 values (Nagelkerke 1991). The Wald statistic (Texler and Travis 1993) was used to evaluate the effects of individual variables in the model. Hosmer and Lemeshow (2000) goodness-of-fit test was conducted to quantify the level of agreement between the estimated and observed values (Gribko et al.1995, Wulder et al. 2006) with $P \geq 0.05$ indicating a good fit. We used Enter method to include independent variables into the regression, where all predictor variables were selected to enter into the equation simultaneously (Maroof 2012).

Prediction Model Development and Validation. The original vineyard variables that contributed significantly to vineyard infestation status, based on the Wald statistic, were again regressed on the response variable (light or heavy infestation) using binary logistic regression to develop a final prediction model. Because interpretation of a logistic regression coefficient, β, is not as straightforward as a linear regression coefficient, the exponential coefficient, e^{β} or odds ratio, was used to interpret the outcome (Norušis 2005). The odds ratio refers to the ratio change in the odds of the event (i.e., infestation status) for a unit change in the predictor variable after taking into account all other predictors in the model (Freund and Wilson 1998, Wulder et al. 2006, Maroof 2012). Odds is defined as the ratio of the probability that an event occurs (in this case, that the block is heavily infested) divided by the probability that it does not (i.e., that the block is not infested or lightly infested; King 2008). Binary logistic regression analyses were conducted using SPSS (IBM Corp. 2012).

In addition, the receiver operating characteristic curve (ROC) was used to assess the predictive ability of the risk prediction model (Hanley and McNeil 1982, Swets 1988, Wong et al. 2004). The ROC is a graphical representation of the relationship between rates of false positives (i.e., incorrectly predicting the positive outcome, known as "sensitivity") and true positives (correctly predicting the positive outcome, known as "1-specificity"; DeLong et al. 1988, Pearce and Ferrier 2000). The area under the ROC curve, AUC, represents the probability of correctly classifying the levels of the dependent variable (in this case, "lightly" or "heavily" infested). The AUC index ranges from 0.5 for models with no discrimination ability to 1.0 for models with perfect discrimination ability. AUC values between 0.5 and 0.7 indicate poor discrimination ability of the model. Values between 0.7 and 0.9 indicate a reasonable discrimination ability of the fitted model and are considered appropriate for many uses, and values >0.9 indicate a very good discrimination capacity of the model (Swets 1988).

Results

Pupal Exuviae Sampling. Pupal exuviae densities varied widely among the vineyard blocks, ranging from 0.0 to 6.4 exuviae per vine in a single year (Fig. 1). The maximum number of exuviae collected from a single vine in 1 yr was 28, from vineyard 32 (Fig. 1).

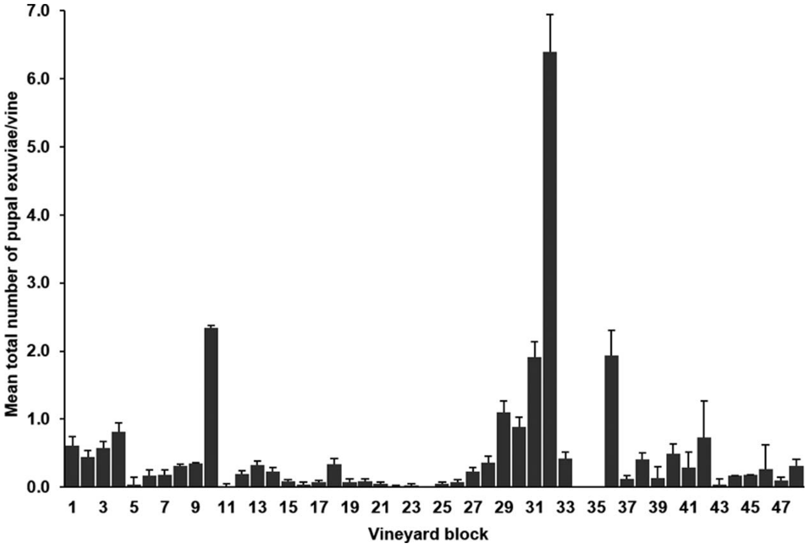

Fig. 1. Seasonal mean ± SE number of grape root borer pupal exuviae per vine collected from 48 vineyard blocks in Virginia.

In the four blocks assessed annually over several consecutive years, the mean number of exuviae per vine declined between 2008 and 2011 in blocks A and B (Fig. 2). In block C, the mean number of exuviae per vine increased and then decreased during the same interval, while they remained essentially the same at block D from 2010 to 2012. In those blocks, the cumulative number of pupal exuviae collected from a single vine over 3–4 yr of sampling ranged from 0 to 19. Except from vineyard blocks A and B in 2011, annual mean pupal exuviae counts per vine was >0.1.

Identification of Risk Factors. Using CATPCA, the 18 nominal, ordinal, and numeric variables were reduced to three PCs by examining the scree plot (Fig. 3). The three PCs accounted for 53.65% of the total variance in the original vineyard variables, with seven of the variables (ground cover, soil texture, soil mass moisture, soil pH, clay/sand ratio, clay/silt ratio, and sand/silt ratio) having loading values of ≥0.70 (Table 1). The CATPCA model summary resulted in a Cronbach's Alpha of 0.949, indicating strong internal consistency among the three PC variables.

Association of Key Vineyard Factors With Infestation. The variable, soil texture, was redundant with the ratios of soil particle size classes (i.e., clay/sand, clay/silt, and sand/silt) and, therefore, was excluded from further analysis. The six remaining variables, which showed significant component loadings, were

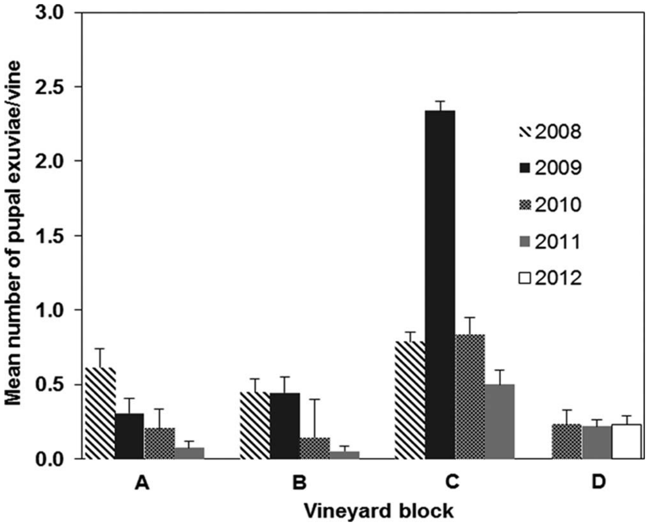

Fig. 2. Mean ± SE number of pupal exuviae per vine from four vineyard blocks in Virginia surveyed in 3–4 consecutive years.

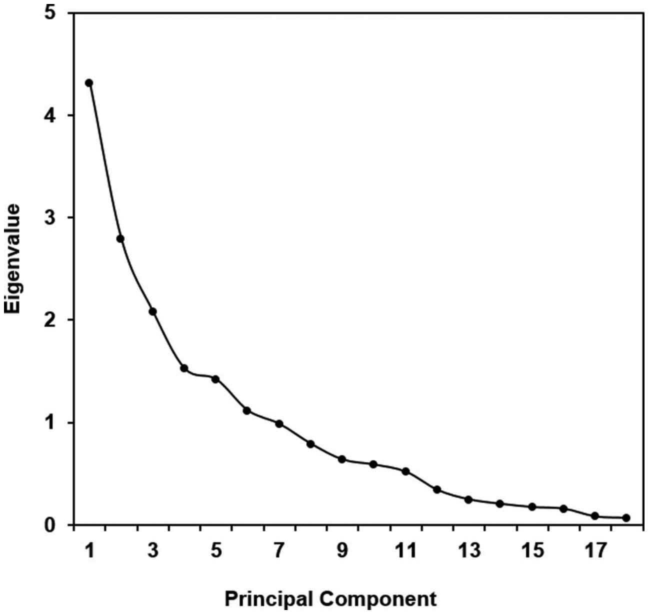

Fig. 3. Scree plot that includes 18 vineyard variables measured in 48 vineyard blocks in CATPCA.

used for binary logistic regression analysis (Table 2). The regression model was significant, based on the omnibus test statistic ($\chi^2 = 13.98$; df = 6; $P = 0.03$), and explained 43.1% of the total variability as indicated by the Nagelkerke r^2 value. Hosmer and Lemeshow (2000) goodness-of-fit test showed that there was no significant difference ($\chi^2 = 1.77$; df = 8; $P = 0.99$) between observed and predicted values. Two variables, soil mass moisture and clay/sand ratio, contributed significantly to infestation status (Table 2).

Based on these results, soil mass moisture and clay/sand ratio were regressed on the binary infestation status categories (i.e., light and heavy infestation). The binary logistic regression model was significant, based on the omnibus test statistic ($\chi^2 = 13.95$; df = 2; $P = <0.001$) and a Nagelkerke r^2 value of 0.35.

Table 1. Mean ± SE and mode of the quantitative and categorical vineyard variables, respectively, collected from 48 vineyard blocks in Virginia, and component loadings obtained from CATPCA

Vineyard variables	Parameters		Principal components		
	Mean ± SE; mode	Range	PC1	PC2	PC3
Horticultural					
Cultivar	Cabernet Franc[a]	NA	−0.444	−0.162	−0.634
Rootstock	C-3309[a]	NA	−0.477	0.610	−0.273
Vine age (yr)	11.55 ± 0.82	2−23	−0.280	0.240	0.523
Planting area (ac)	3.49 ± 0.45	0.25−11.45	0.128	−0.046	−0.449
Cultural					
No. insecticide sprays	2.33 ± 0.26	0−5	−0.350	0.363	−0.620
Irrigation	No[a]	1−2[b]	0.055	−0.205	−0.168
Ground cover	1[a]	1−2[b]	−0.114	0.767*	0.391
Weed control	2[a]	1−4[b]	0.023	−0.342	−0.070
Environmental					
Distance to forest (m)	73.13 ± 15.73	1.94−551.74	0.125	0.052	−0.018
Bulk density (g/cm^3)	1.22 ± 0.01	0.97−1.42	−0.483	−0.119	−0.206
Mass soil moisture (%)	23.75 ± 0.60	14.63−35.45	0.911*	−0.161	−0.032
Soil texture	Silty loam[a]	NA	−0.795*	−0.452	0.225
Soil pH	6.24 ± 0.07	4.70−7.12	−0.070	−0.051	−0.795*
Soil organic matter (%)	3.17 ± 0.12	1.50−4.90	0.640	0.388	−0.033
CEC (cmol+/kg)	6.52 ± 0.24	3.70−10.60	0.657	−0.172	−0.355
Clay/sand ratio	0.84 ± 0.09	0.13−3.53	0.704*	0.424	−0.124
Clay/silt ratio	0.53 ± 0.04	0.19−1.41	0.080	0.892*	−0.179
Sand/silt ratio	0.77 ± 0.06	0.23−1.58	−0.811*	0.320	−0.053
Eigenvalues	–	–	4.386	2.845	2.425
Variance (%)	–	–	24.37	15.81	13.47

[a] Mode.

[b] Ranking – Ground cover: 1, ≤40%; 2, >40% cover around vine base; weed control: 1, none; 2, light; 3, medium; 4, aggressive.

Asterisk indicates component loadings with values ≥0.70.

Table 2. Binary logistic regression parameters and associated statistics derived from an analysis using six selected predictor variables measured from 48 vineyard blocks in Virginia

Variables	β	SE	Wald χ^2	df	P-value	Odds ratio (e^{β})
Soil mass moisture	−0.542	0.259	4.380	1	0.036	0.582
Ground cover	−0.671	1.024	0.430	1	0.512	0.511
Soil pH	1.036	1.113	0.867	1	0.352	2.819
Clay/sand ratio	9.746	4.813	4.100	1	0.043	17091.49
Clay/silt ratio	−9.322	5.102	3.339	1	0.068	0.00
Sand/silt ratio	5.009	4.266	1.378	1	0.240	149.68
Constant	2.158	11.328	0.036	1	0.849	8.65

Omnibus test statistic (χ^2 = 13.98; df = 6; P = 0.03). Nagelkerke r^2 = 0.431.

Hosmer and Lemeshow"s (2000) statistic ($\chi^2 = 15.08$; df = 8; $P = 0.06$) indicated a good fit of the model. The effect of soil mass moisture was significant based on the Wald test (χ^2 = 8.46; df = 1; P = 0.004) and was negatively associated with infestation status. The clay/sand ratio was also significant (χ^2 = 6.54; df = 1; P = 0.01), but positively associated with infestation status (Table 3). The intercept or constant of the model was also significantly different from zero (χ^2 = 7.75; df = 1; $P = 0.005$). The odds ratio, e^{β}, for soil mass moisture and clay/sand ratio were 0.68 and 25.63, respectively (Table 3).

Prediction Model. Based the results of regression analyses, the relationship between the significant, original vineyard variables, and the probability of a vineyard block being infested by grape root borer was calculated using the equation,

$$\pi(x) = \frac{e^{[7.425\,-\,0.392\,(\%\ soil\ mass\ moisture)\,+\,3.244\,(clay\ to\ sand\ ratio)]}}{1 + e^{[7.425\,-\,0.392(\%\ soil\ mass\ moisture)\,+\,3.244\,(clay\ to\ sand\ ratio)]}} \quad [1]$$

where $\pi(x)$ is the probability of an infestation by grape root borer larvae in a vineyard block. Figure 4 shows the results of using the model in equation 1 to predict the probability that a vineyard block will be infested by grape root borer larvae, based on the combined effects of soil mass moisture and the clay/sand ratio. The AUC value of 0.80 indicated a good predictive ability of the model. In the ROC (Fig. 5), the best cutoff point (shown by the arrow), which lies closest to the top left corner of the ROC space, is the point where the model sensitivity and specificity are optimal.

Table 3. Binary logistic regression parameters and associated statistics derived from the analysis using the two final predictor variables measured from 48 vineyard blocks in Virginia

Variables	β	SE	Wald χ^2	df	P-value	Odds ratio (e^{β})
Soil mass moisture	−0.392	0.135	8.46	1	0.004	0.68
Clay/sand ratio	3.244	1.268	6.54	1	0.011	25.63
Constant	7.423	2.666	7.75	1	0.005	1674.03

Omnibus test statistic (χ^2 = 13.95; df = 2; P = <0.001). Nagelkerke r^2 = 0.345.

Discussion

This study has provided the most comprehensive assessment of vineyard infestation by larvae of grape root borer yet reported. Three of the 48 vineyard blocks selected for the study yielded no pupal exuviae, while the remaining blocks were infested to widely varying degrees (Fig. 1). In the most heavily infested block, we witnessed the removal of several vines and counted between 14 and 39 live larvae per vine on only the exposed portion of the root system. Those plants were in significant decline and vine losses were occurring. However, despite the frequency of vineyard infestation that we recorded and the fact that many vines in the blocks sampled in consecutive years yielded pupal exuviae each year (Fig. 2), most blocks did not show overt signs of problems that were of immediate concern to the vineyard managers.

The pronounced differences in pupal exuviae density among vineyard blocks (Fig. 1) raises the important question of whether the blocks that were not infested or lightly infested would become heavily infested over time. Sampling of the same vines in several infested blocks over 3–4 consecutive seasons revealed instances in which annual mean pupal exuviae counts per vine decreased, increased, or remained static (Fig. 2), which may have been due to annual differences in environmental conditions (e.g., rainfall) or other factors when the eggs were laid, two years before each survey year. As well, the differences among blocks that were revealed by our sampling provided a strong basis for a comparison of putative risk factors among them.

The effects of various abiotic and biotic factors on populations of other root-feeding herbivorous insects have been reported (Strnad and Bergman 1987, Brown and Gange 1990, Villani and Wright 1990, Erb and Lu 2013), although we are not aware of another study that included as many variables as were used in the present research. None of the horticultural or cultural factors examined were significantly associated with grape root borer infestations. Of the environmental factors evaluated, no effect of vineyard proximity to forested areas was observed. Using the same pupal exuviae data, Rijal et al. (2014) measured the spatial distribution of infestations. Despite aggregated distributions in blocks with ≥0.5 pupal exuviae per vine, there were no indications that populations were higher or aggregated at the edges of the blocks, although Hoffman and Dennehy (1989) reported higher infestations of grape berry moth, *Paralobesia viteana* (Clemens), in border rows of the vineyards with wild vines nearby.

As mentioned previously, grape root borer infestations are ultimately dependent upon neonates finding and establishing on grape roots. Rijal et al. (2013) showed that grape root volatiles may have an important role in larval food-finding, although the current study revealed no effects of rootstock. Soil texture, moisture, porosity, particle size, and compaction can affect the dispersion of behaviorally active host stimuli chemicals in the rhizosphere and also may influence the mobility and survival of root-feeding insect larvae (Villani and Wright 1990, Gregory and Johnson 2006).

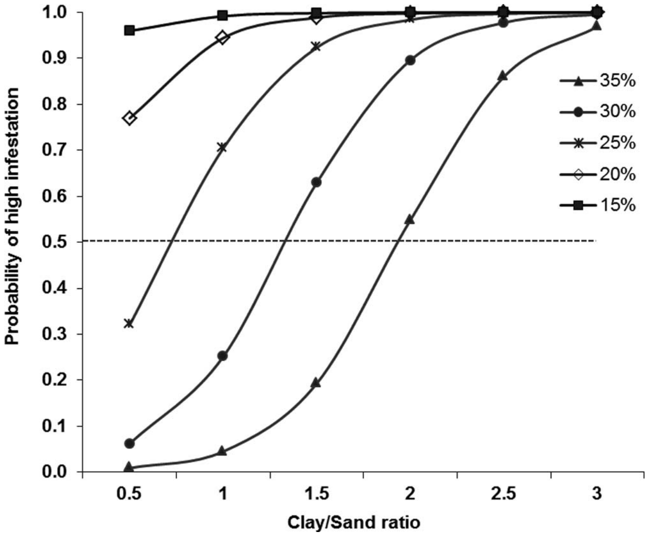

Fig. 4. Predicted probability of high grape root borer infestation in vineyard blocks calculated using hypothetical values of predictors (i.e., percent soil mass moisture and clay/sand ratio) in a risk prediction model. The lines represent the probability values for different soil mass moisture levels.

Very low and high soil moisture content is unfavorable for young larvae of root-feeding insects (Macdonald and Ellis 1990, Erb and Lu 2013). Sarai (1972) showed that 0, 20, and 30% soil moisture caused 100, 65, and 50% mortality, respectively, of grape root borer larvae seeking grape roots buried ≈10 cm deep in soil. We found that soil mass moisture, a measure of the ability of the soil to retain water, was negatively related to infestations within the range of values measured (15−35% mass moisture). The four most heavily infested blocks (i.e., with >1 pupal exuviae per vine) had a mass moisture range of 18−20%, while five blocks that were relatively lightly infested (mean of 0.098 pupal exuviae per vine) had soil mass moisture values of 30−35%. This negative association may have been owing to the high number of soil pore spaces filled with water. Godfrey and Yeargan (1985) reported that 35% soil moisture content significantly

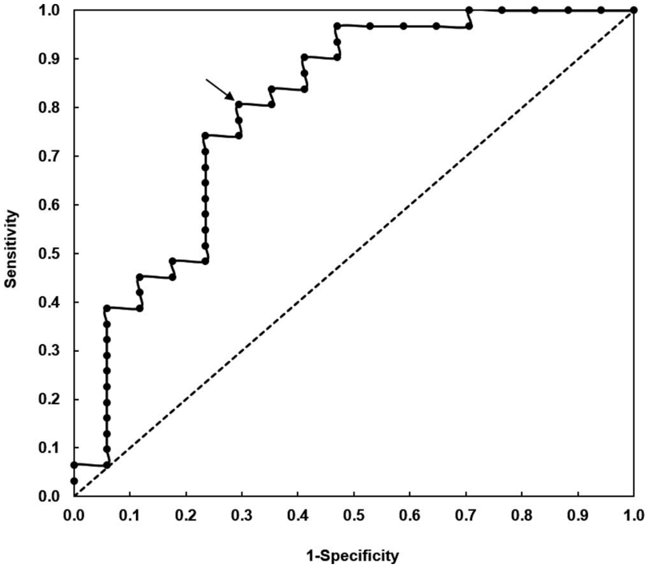

Fig. 5. ROC curve showing the relationship between the true-positive rate (sensitivity) and the false-positive rate (1-specificity) when vineyard blocks were assigned to two groups ("heavily" and "lightly" infested). The area under the ROC curve (AUC) represents the probability of correctly distinguishing between the two groups. The arrow shows the optimal point for sensitivity and specificity, and the dashed line represents a hypothetical ROC curve indicating no discrimination ability of the model.

reduced the survivorship of larval clover root curculio, *Sitona hispidulus* (F.), on alfalfa. Ladd and Buriff (1979) reported significantly higher mortality of Japanese beetle larvae, *Popillia japonica* Newman, in soil at 90% compared with 60% of field water capacity moisture. Significant damage by wireworms in green cover crops was reported when soil moisture was <25% of saturation (cited in Lees 1943). Soil moisture >30% in the study reported here may have hindered the movement of grape root borer neonates through the soil (Lees 1943, Macdonald and Ellis 1990) and thus influenced their food-finding behavior (Coleman et al. 2004).

We also found that soils with higher clay/sand ratios within the range of 0.5–3.0, which corresponded to finer soil types, were positively associated with grape root borer infestations. Larvae of western corn rootworm, *Diabrotica virgifera virgifera* LeConte, were found to move three times faster in silty clay or loam compared with loamy sand soil (Macdonald and Ellis 1990). Similarly, Brust and House (1990) reported lower larval survival of southern corn rootworm, *Diabrotica undecimpunctata howardi* Barber, in soil with low clay content.

Although we did not assess the potential contribution of entomopathogenic nematodes to differences in the extent of grape root borer infestation among blocks, Williams et al. (2010) showed that at least two species of native, soil-dwelling nematodes attacked larval grape root borer and that their effectiveness varied with species, location, soil texture, and soil moisture content. Interestingly, some studies have shown an inverse relationship between soil clay content and the occurrence of entomopathogenic nematodes, while sand and silt content were positively associated with nematode occurrence (Kung et al. 1990, Koppenhöfer and Fuzy 2006, Campos-Herrera et al. 2008). Based on our results and those from the aforementioned studies, soil conditions that promote grape root borer infestations may not be optimal for entomopathogenic nematodes, suggesting that the relationships between nematodes, larval grape root borer, and soils in commercial vineyards is an important question for future research.

The risk prediction model presented here can be used to estimate the probability of a vineyard being or becoming infested by grape root borer larvae, using site-specific values for percent soil mass moisture and clay/sand ratio in the equation The odds ratio (Table 3) for soil mass moisture (0.68) predicts the likelihood that a vineyard block will be highly infested, based on our criterion of >0.10 pupal exuviae per vine. With every unit increase in percent soil mass moisture and with clay/sand ratio held constant, this likelihood is decreased by 0.68 times. Similarly, with every unit increase in the clay/sand ratio with percentage soil mass moisture held constant, the likelihood of a vineyard block being classified as highly infested is increased by >25 times (odds ratio = 25.63). The AUC index of the ROC curve of ≈0.80 indicated that the model can provide good predictions (Swets 1988) of the probability of grape root borer infestations in vineyards in Virginia.

Given the long-standing issue with grape root borer infestations remaining unnoticed until symptoms become apparent (Brooks 1907, Dutcher and All 1979b), the ability of grape growers to predict the likelihood that problems may arise is a key component toward the sustainable management of this pest (Bergh 2012). With further validation, the model developed here may be useful for predicting the likelihood that an established vineyard block is infested by grape root borer, thereby aiding its management by prompting population assessments. At new vineyard sites, the model may provide a better understanding of the relative risk from this pest and spur the vigilance that is often lacking, but necessary, to mitigate the development of damaging populations at some sites. In combination with this model, the recent development of a quantitative sampling protocol for grape root borer (Rijal et al. 2014) and the registration of a mating disruption formulation, have significantly advanced our capacity to advise eastern grape growers about preventing or managing the ongoing problems associated with this pest. Research on economic injury levels and action thresholds for grape root borer on different grape species and rootstocks and the role of nematodes in its biological control will further enhance the development of integrated pest management recommendations.

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