Estimation of Feeding Threshold for *Homalodisca vitripennis* (Hemiptera: Cicadellidae) and Its Application to Prediction of Overwintering Mortality

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ABSTRACT The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), vectors the bacterium *Xylella fastidiosa* that induces Pierce's disease of grape. This study determined the effect of temperature on the feeding activity of *H. vitripennis* adults and the resulting production of excreta. The Logan type I model described a nonlinear pattern that showed excreta production increased up to an optimal temperature (33.1°C), followed by an abrupt decline near an estimated upper threshold (36.4°C). A temperature threshold for feeding, at or below which adults cease feeding, was estimated to be 10°C using a linear regression model based on the percentage of adults producing excreta over a range of constant temperatures. A simulated winter-temperature experiment using fluctuating thermal cycles confirmed that a time period above the temperature threshold for feeding was a critical factor in determining adult survival. Using data from the simulated temperature study, a predictive model was constructed by quantifying the relationship between cumulative mortality and cooling degree-hours. In field validation experiments, the model accurately predicted the temporal pattern of overwintering mortality of *H. vitripennis* adults held under winter temperatures simulating conditions in Bakersfield and Riverside, California, in 2006–2007. Model prediction using winter temperature data from a Riverside weather station indicated that *H. vitripennis* adults would experience an average of 92% overwintering mortality before reproduction in the spring, but levels of mortality varied depending on winter temperatures. The potential for temperature-based indices to predict temporal and spatial dynamics of *H. vitripennis* overwintering is discussed.

KEY WORDS glassy-winged sharpshooter, feeding, temperature, overwintering, mortality

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), is an important vector of *Xylella fastidiosa* Wells et al., a bacterial pathogen that causes scorch-like diseases in agricultural and landscape plants (e.g., grape, almond, and oleander) (Hopkins and Purcell 2002, Redak et al. 2004). *H. vitripennis* was found in southern California in the mid-1980s (Sorensen and Gill 1996), and later associated with an increase in Pierce's disease incidence in vineyards located within infested areas (Blua et al. 1999, Sisterson et al. 2008). Whereas both *X. fastidiosa* and native vectors have been present in California for over 100 yr (Freitag et al. 1952, Davis et al. 1980), the presence of *H. vitripennis* combined with the ubiquitous nature of the pathogen (Shapland et al. 2006) posed a new and greater threat. Compared with leafhopper vectors native to California, *H. vitripennis* has a wide host range (Hoddle et al. 2003) and long flight period (Blua and Morgan 2003), which increases its dispersal capabilities. Additionally, some portion of the *H. vitripennis* population feeds on and transmits *X. fastidiosa* to the mature basal portion of the grape cane, which may lead to higher *X. fastidiosa* overwintering survival because bacterial infections cannot be eliminated by either winter curing or pruning (Almeida and Purcell 2003, Park et al. 2006).

In California, *H. vitripennis* populations are presently established in the southern coastal and interior valleys, and the southern region of the San Joaquin Valley (CDFA 2008). The northward range expansion of this pest is a concern because this poses a greater risk for the northern California grape and almond industries. Previous studies reported that the native

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range of *H. vitripennis* includes the southeastern United States and northeastern Mexico (Triapitsyn and Phillips 2000). Based on predictions generated by the CLIMEX program, Hoddle (2004) suggested that winter cold stress would prevent *H. vitripennis* from establishing permanent populations north of California. However, one drawback of using the CLIMEX model is that when there are no biological parameters on the target species, the model parameters must be estimated from an inverse (or inferential) modeling process by manually adjusting parameter values until the simulated geographical distribution coincides with the observed distribution (Vera et al. 2002). Such was the case with *H. vitripennis* and, therefore, the northward expansion may be more or less limited by winter temperatures than predicted by current CLIMEX estimates. Winter temperatures would also impact this pest's population densities. Because *H. vitripennis* adults overwinter without diapause (Turner and Pollard 1958), they are required to periodically feed on plants and their survival is likely affected by low temperatures, as seen in other insects (Bale 1991, Leather et al. 1993). Therefore, in addition to limiting *H. vitripennis*'s geographic distribution, winter temperatures may reduce overwintering success in regions where the pest is established and influence *H. vitripennis* population densities the following year.

In the laboratory, Son et al. (2009) showed that adult *H. vitripennis* survival was negatively influenced by prolonged exposure to temperatures ≤7.8°C, independent of the availability of suitable host plants. They hypothesized that long-term exposure to low temperatures would impede *H. vitripennis* feeding and, as the insect starves, it would suffer dehydration, depletion of energy reserves, and ultimately death. There are also field observations to support this hypothesis. In southern California, adult *H. vitripennis* densities gradually declined through the winter months (Blua et al. 2001, Castle et al. 2005). Similarly, Pollard and Kaloostian (1961) observed that *Homalodisca liturata* (Ball) adults remained sessile, without feeding, at temperatures <11.1°C.

Temperature is a major abiotic factor affecting various aspects of an insect's biology (Gilbert and Raworth 1996), and its direct effects are often the key determining factor for survival because insects are poikilotherms with their metabolic rates strongly influenced by ambient temperatures (Speight et al. 1999). However, we know of no published reports that describe the influences of temperature on *H. vitripennis* feeding, other than our previous study (Son et al. 2009). This information is needed to fully understand this pest's feeding behavior in relation to pathogen transmission, predict its seasonal population dynamics, and delimitate its potential geographic distribution. In this study, we investigated the impacts of temperature on adult *H. vitripennis* feeding and survival. The objectives were to: 1) determine the temperature threshold at or below which feeding does not occur; 2) develop a predictive model based on the relationship between the low temperatures, feeding activity, and the resulting *H. vitripennis* survival; and 3) validate the predictive model in a field situation by simultaneously monitoring temperature and overwintering survival.

Materials and Methods

Insects and Plants. Unless otherwise stated, laboratory-reared *H. vitripennis* adults (≈3 wk old) used in this study were obtained from the California Department of Food Agriculture Biocontrol Facility (Arvin, CA). At the California Department of Food Agriculture facility, the laboratory colony of *H. vitripennis*, originally collected mainly at citrus orchards in Ventura County, has been maintained to harvest *H. vitripennis* eggs to produce biological control agents (egg parasitoids) against *H. vitripennis*. The adults were transferred and maintained in screened cages (Bioquip Products, Gardena, CA) provisioned with potted plants of cowpea (*Vigna unguiculata* [L.] Walp) and 'Frost Eureka' lemon (*Citrus limon* [L.] Burm. f.) at an enclosed *H. vitripennis* laboratory at California State University, Fresno. Insecticide-free lemon plants were obtained from the United States Department of Agriculture-Agricultural Research Service San Joaquin Valley Agricultural Sciences Center (Parlier, CA), and individually transplanted into pots (3.78 liter), which were then maintained in a greenhouse at the University of California Kearney Agricultural Research and Extension Center (Parlier, CA). Lemon trees were used as a feeding host because they were a common year-round host for *H. vitripennis* in southern California (Perring et al. 2001) and did not show visible stress symptoms caused by low or high temperatures in a previous study (Son et al. 2009).

Determination of Feeding Thresholds: Constant Temperatures. Subsistence on nutrient-sparse (<5%) xylem requires *H. vitripennis* to ingest large volumes of xylem fluid, and this behavior produces large volumes of liquid excreta (Andersen et al. 1989), which has been used to measure feeding activity (Brodbeck et al. 1993). Similarly, we used excreta-collection sachets to estimate levels of *H. vitripennis* feeding activity. A sachet (7.5 × 6.5 cm) was made from Parafilm (VWR Lab, Batavia, IL) by the method of Pathak et al. (1982). Adults were individually captured within a rearing cage using a clear plastic vial (33 ml; Bioquip Products, Gardena, CA), and their gender was determined. Adult males and females were individually placed in the sachet, which was then enclosed around the stem of a potted lemon plant (1 m height) and sealed. Plants were then randomly allocated to constant temperature treatments in environmental chambers set at 8.9, 13.3, 18.8, 21.7, 24.6, 31.1, 35.1, and 40.8 ± 1°C, as monitored using a data logger (HOBO, Onset Computer, Bourne, MA), with a photoperiod of 10:14 (L:D) h. The lemon plants were watered daily until the potting soil became fully saturated. After a 48-h feeding period, the excreta produced was measured (in mg) using an electronic balance (weight of sachet with excreta – initial weight of sachet). Adult survival during the 48-h feeding period was also determined.

Statistical Analysis. Data presented in this work are mean values (±SEM). One insect per host plant was considered a replicate, and each treatment had 10–12 replicates per sex. Before statistical analysis, data on the weight of xylem excreta were transformed ($\log_{10}[x + 1]$) to normalize variance. Treatment effects were determined using a mixed model analysis of variance (ANOVA) (SAS Institute 1995); treatment means were separated using the Student-Newman-Keuls test. χ^2 analysis was used to determine the treatment effect on the frequency of adults that produced xylem excreta and survived the 48-h trial. Regression analysis was performed to estimate model parameters for temperature effects on each response variable using the TableCurve 2D Curve Fitting Program (Jandel Scientific 1996).

Temperature-Dependent Feeding Model. The relationship between temperature and the percentage of *H. vitripennis* adults that produced xylem excreta during the 48-h trial was described using a two-parameter Weibull distribution model (Cockfield et al. 1994) as follows:

$$P(T) = 100 - 100 \times \exp[-(T/\alpha)^{\beta}] \qquad [1]$$

where $P(T)$ is the percentage of adults that produced excreta; α and β are scale and shape parameters, respectively. By using the linear portion of the nonlinear curve, the lower threshold temperature was estimated from a linear model (Campbell et al. 1974).

The temperature-dependent trend for excreta production was quantified as a function of temperature using a combination of the nonlinear Logan type I model (Logan et al. 1976) and the linear model. Before regression, the amount of excreta produced hourly per adult was calculated by dividing the excreta amount per surviving adults by 48-h confinement time. The Logan model was used to fit the data over the full range of the test temperatures, and the mathematical expression was as follows:

$$Y(T) = \psi\{\exp(\rho T) - \exp[\rho T_L - (T_L - T)/\Delta T]\} \qquad [2]$$

where $Y(T)$ is the amount of xylem excreta produced at temperature T, ψ is a measurable amount of the excreta production at an arbitrary base temperature, ρ can be interpreted as a composite Q_{10} value for enzyme-catalyzed biochemical reactions, T_L is the lethal maximum temperature, and ΔT is the width of the decline phase above the optimum temperature.

Development of a Predictive Survival Model: Fluctuating Temperatures. To verify the validity of the feeding threshold estimated from constant temperatures, adults were held under fluctuating temperature regimes, selected to simulate realistic hourly cycles of three California sites in winter. Under a photoperiod of 10:14 (L:D) h, temperature-controlled environmental chambers were programmed to simulate the hourly temperature cycles in three geographically distant locations in California: 1) Riverside (Riverside County) in the Los Angeles Basin region where *H. vitripennis* populations are well established; 2) Oakville (Napa County) in the North Coast region, where *H. vitripennis* is likely to establish because of mild winters; and 3) Buntingville (Lassen County) in the Northeast Plateau region, where the pest is unlikely to establish as a result of harsh winter temperatures. The environmental chambers were set to simulate hourly cycles of a typical winter day (i.e., 1 January 2006) for each location, excluding temperatures at or below 0°C to ensure that we were measuring the effects of low temperature inactivity instead of freezing on the test insects. Hourly temperature data were obtained from the California Irrigation Management Information System website (http://www.cimis.water.ca.gov). The geo-references (elevation, latitude, and longitude) for the weather stations are Riverside (311 m, 33°57′ N, 117°20′ W), Oakville (58 m, 38°26′ N, 122°24′ W), and Buntingville (1,221 m, 40°17′ N, 120°26′ W). To record the actual treatment temperatures experienced by the insects, a data logger (HOBO, Onset Computer, Bourne, MA) was installed in each environmental chamber.

A cylindrical cage (15 cm diameter × 75 cm height) made of clear plastic sheeting (PETG-Vivak) was placed over top of each of nine potted lemon plants used in the study. The cages had a screened top and two ventilation holes (2.5 cm diameter) in the wall. Ten laboratory-reared young adults were transferred into each cylinder cage, and each cage was considered a replicate. This experiment had three treatments (three thermal profiles) with three replicates per treatment. The number of surviving adults was checked every 2 d during 5 wk after exposure, and then every 7 d until all adults in all replications were dead. Treatment effects were determined using repeated measures ANOVA (SAS Institute 1995). This experiment was designed to determine the effect of fluctuating and nonfreezing field temperatures on adult survival, and results were then used to develop a predictive model (below), based on the relationship between duration of starvation below the feeding threshold and resulting survival.

Cooling Degree-Hours Model. A quantitative model was developed to describe the relationship between the period (hourly) of nonfeeding (i.e., starvation) below the estimated temperature threshold for feeding (10°C, see "Results") and cumulative mortality of *H. vitripennis* adults. The mean values of mortality (%) obtained from the simulated temperature experiment were plotted against the cumulative cooling degree-hours (CDH), which accounts for hours of starvation as a result of cold exposure below the feeding threshold as a unit of time-temperature. The calculation method of CDH is as follows:

$$CDH_{cumulative} = \Sigma CDH \qquad [3]$$

$$CDH = \begin{bmatrix} T_h - 10°\text{C}, & \text{If } T_h < 10°\text{C} \\ 0, & \text{If } T_h < 10°\text{C} \end{bmatrix} \qquad [4]$$

where T_h is hourly temperature (°C) and $CDH_{cumulative}$ is cumulative CDH. Using the TableCurve 2D Program, a nonlinear regression model was developed to describe the relationship between CDH and percent

mortality by fitting the data to the Weilbull equation (equation 1 provided above). Before regression analysis, the mortality data were plotted against the cooling degree-hours for each treatment.

Validation of the Predictive Model: Field Conditions. *Field Monitoring of Overwintering Survival.* To validate the CDH model, field-cage experiments were conducted at two locations from late November 2006 to early March 2007 using *H. vitripennis* adults that were collected at citrus orchards at Fillmore in Ventura County, California, on 28 November. Upon collection, the adults were transferred to the California Department of Food Agriculture Arvin Facility and held in a cage containing potted cowpea plants at room temperature for 1 d to eliminate individuals that died because of stress during the field collection. Twenty-five adults were collected, using an aspirator, into each plastic vial (33 ml; Bioquip, Gardena, CA), which were then wrapped in paper towels and held in a cooler (≈15°C) during transportation to the study sites. As a result of regulatory protocols and growers' concerns, these field experiments were conducted in Bakersfield at the University of California Kern County Extension Office (elevation: 115 m, 35°20′ 46″ N and 118°57′ 55″ W) and Riverside at the University of California Citrus Experiment Station (elevation: 300 m, 33°57′ 59″ N and 117°20′ 46″ W). *H. vitripennis* populations were naturally present at each site, but winter temperatures differed between the sites.

To meet areawide control concerns, insects were double caged to prevent accidental escape. Test cages were composed of cylindrical iron-wired frames (35 cm diameter × 1.5 m height × 4 cm mesh size) covered by a screen bag with a zipper to allow access. One week before *H. vitripennis* were introduced, cages were attached to the top of individual pots (38 liter), each planted with one grape (*Vitis vinifera*, 'Pinot Noir') and one citrus (*Citrus* spp., 'Camizo') plant. Three caged pots with host plants were placed inside an outer screened tent (2.4 m × 2.4 m × 2.4 m), in which a yellow sticky trap and a noncaged potted citrus plant treated with imidacloprid were placed to trap and kill any escaping insects. Groups of 50 adults were released into each cage on 29 November 2006. A data logger (HOBO, Onset Computer, Bourne, MA) was placed inside a test cage in each outer-tent cage to monitor hourly temperatures. Each site had a total of three outer tents and nine test cages. The number of surviving adults was monitored every 7 d until the end of February 2007. Insects were checked in the afternoon when warmer temperatures increased insect activity and facilitated differentiating between live and dead insects. To aid visual inspection, white play sand was layered on the soil surface in the pots and plant debris was removed during each observation. Potted plants were irrigated routinely and did not exhibit drought symptoms during the experimental period. For data analysis, the mean numbers of surviving adults were transformed ($\log[x + 1]$) to normalize the variance, and treatment effects were compared using repeated measures ANOVA.

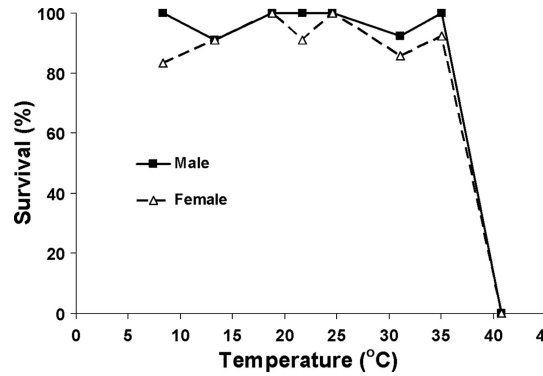

Fig. 1. Survival (%) of *H. vitripennis* adults in 48-h feeding trial under constant temperatures using the Parafilm sachet method.

Prediction Versus Observation Values. For each outer-tent cage, the temperature data were used to calculate the CDH to predict the mortality data because of differences in temperatures among the cages within the same site. Mean (±SEM) observed mortality recorded from the three test cages inside each outer cage, and the predicted mortality data were plotted against calendar date. Because temperature data from one of the data loggers at each site were unavailable because of technical problems, two sets of data per site were used to validate the predicted mortality. Predicted and observed values on each observation date were compared using Wilcoxon paired-sample test after pooling four sets of data at the 5% significance level.

Overwintering Mortality: Estimation Using Weather Data. California Irrigation Management Information System weather station data were used to estimate the overwintering survival of *H. vitripennis* in Riverside (weather station at 310 m [elevation], 22°57′ 54″ N and 117°20′ 08″ W). The value of the lower temperature threshold (10°C) was used to calculate the CDH using hourly ambient air temperature during the *H. vitripennis* overwintering period (i.e., November-February) in each year, for nine winter seasons. The cumulative CDH during this period was used as input data to estimate the overwintering mortality on corresponding calendar dates because reproduction of overwintered females begins in early March in Riverside (Hummel et al. 2006).

Results

Constant Temperature Experiment. *Adult Survival.* Temperature significantly influenced adult survival ($\chi^2 = 119.02$, df = 7, $P < 0.0001$), but insect sex was not a factor ($\chi^2 = 0.48$, df = 1, $P > 0.05$) (Fig. 1). Survival of *H. vitripennis* adults was >80% at all temperatures except 40.8°C, a temperature at which all of the tested adults died in the 48-h trial. Forty of the 194 adults tested did not survive the trial. Among them, five adults drowned in their own excreta (1, 1, 1, and 2 adults at 21.7, 24.6, 31.7, and 35.1°C, respectively) and these data were excluded from the analysis.

Table 1. Excreta production per *Homalodisca vitripennis* adult during 48-h feeding on 'Eureka' lemon plants at constant temperatures

Temp (°C)	N^a	Mean ± SEM excreta (mg)					
		n	Male	*N*	Female	*n*	Total
8.3	23	11	0.0 ± 0.0c	10	0.0 ± 0.0e	21	0.0 ± 0.0e
13.3	22	10	0.0 ± 0.0c	10	47.8 ± 47.8de	20	23.9 ± 23.9e
18.8	23	11	105.6 ± 98.1c	12	340.7 ± 323.3cd	23	228.2 ± 173.1d
21.7	21	10	325.6 ± 140.9b	10	712.2 ± 310.0bc	20	518.9 ± 171.6c
24.6	25	12	1,766.5 ± 987.6a	12	2,302.0 ± 1,027.6ab	24	2,034.2 ± 699.2b
31.1	27	12	2,993.9 ± 931.9a	12	6,932.0 ± 2,384.3a	24	4,963.0 ± 1,317.5a
35.1	25	10	4,156.6 ± 1,286.4a	12	4,025.0 ± 2,064.1ab	22	4,084.8 ± 1,240.9ab
40.8	24	0	—[b]	0	—	0	—

Means followed by the same letter within each column are not significantly different (Student-Newman-Keuls test, $P < 0.05$).
[a] Total number of tested adults per treatment.
[b] Data unavailable due to 100% mortality.

Excreta Production. Among the temperature treatments 13.3–35.1°C, the percentage of adults that produced excreta was significantly different ($\chi^2 = 131.58$, df = 7, $P < 0.0001$), but did not vary between sex ($\chi^2 = 1.69$, df = 1, $P > 0.05$). At 24.6–35.1°C, all *H. vitripennis* adults produced excreta. The percentage of adults producing excreta declined as temperature decreased. At temperatures ≤13.3°C, only one of 41 adults tested produced excreta. The excreta production per *H. vitripennis* adult surviving the 48-h trial was highly dependent upon temperature ($F = 234.9$; df = 6, 153; $P < 0.001$), but there was no difference between sexes ($F = 0.47$; df = 1, 153; $P > 0.05$) or interaction between temperature and sex ($F = 0.50$; df = 6, 153; $P > 0.05$) (Table 1). Therefore, data from males and females were pooled for regression analysis. No adults produced excreta at temperatures ≤8.3°C. The amount of excreta per *H. vitripennis* adult increased until it peaked at 31.1°C. High variation in excreta production among individuals was observed at 35.1°C, ranging from 7.2 to 25,241.7 mg.

Temperature-Dependent Feeding Model. The Weibull model (equation 1) accurately described the nonlinear relationship between temperature and the percentage of *H. vitripennis* adults that produced excreta over the temperature range from 8.3 to 35.1°C ($F = 111.27$; df = 1, 6; $P < 0.001$) (Fig. 2; Table 2). At 13.7, 15.9, 18.0, and 19.9°C, for instance, it was predicted that 10, 25, 50, and 75% of surviving *H. vitripennis* adults would produce excreta, respectively. A linear model was successfully fitted to the data from the linear portion (8.3–24.6°C) of the nonlinear Weibull curve ($F = 45.34$; df = 1, 4; $P < 0.01$) (Table 2) and provided an estimate (axis intercept) of a lower feeding threshold temperature of 10.0°C.

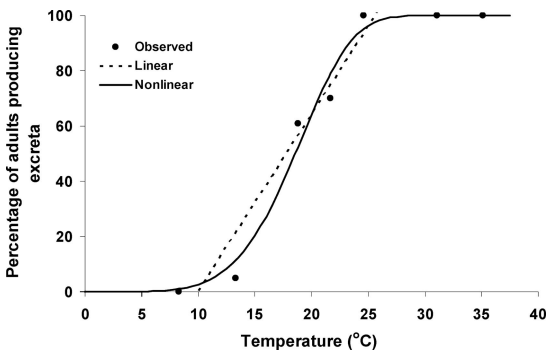

Fig. 2. Temperature-dependent frequency (%) of *H. vitripennis* adults that produced the excreta for 48-h trial as fitted to the nonlinear Weibull model.

Hourly excreta production, estimated by dividing total excreta production per adult by 48 h, was influenced by a temperature main effect ($F = 25.30$; df = 6, 153; $P < 0.001$), but without a significant gender ($F = 0.15$; df = 6, 153; $P > 0.05$) or interaction (temperature × gender) effect ($F = 0.49$; df = 6, 153; $P > 0.05$). The effect of temperature on hourly excreta production per adult was well described by the nonlinear Logan model over the entire temperature range ($F = 71.20$; df = 3, 6; $P < 0.01$) (Fig. 3; Table 3). This nonlinear model estimated 33.1°C as the temperature with the highest mean excreta production (117.8 mg/h) and 36.4°C as the upper threshold temperature. Excreta production increased gradually up to 21.7°C and then sharply increased to the optimal temperature, followed by an abrupt decline at temperatures between the predicted optimal (33.1°C) and upper threshold (36.4°C) temperatures. A linear model generated from all data at temperatures ≤31.1°C estimated a lower threshold of 13.3°C with a significant positive linear relationship with temperature ($F = 10.90$; df = 1, 5; $P < 0.05$) (Fig. 3; Table 3).

Simulated Temperature Experiment. The mean (±SEM) temperatures for the 24-h profiles were 12.0 ± 0.3°C (range: 10.1–14.4°C), 10.5 ± 0.4°C (range: 6.8–12.6°C), and 3.3 ± 0.3°C (range: 1.3–7.9°C) for the temperature regimes simulating conditions in Riverside, Oakville, and Buntingville, respectively (Fig. 4A). Xylem excreta production was observed under

Table 2. Parameter estimates of models to describe the relationship between temperature and the percentage of *Homalodisca vitripennis* adults that produced xylem excreta during 48-h trial

Model	Parameter	Estimate ± SEM	r^2
Nonlinear Weibull model	α	18.9807 ± 0.6441	0.957
(Cockfield et al. 1994)	β	6.9183 ± 2.5487	
Linear model[a]	a	−63.7779 ± 17.3926	0.938
(Campbell et al. 1974)	b	6.3986 ± 0.9501	

[a] Data range 8.3–24.6°C was chosen for the linear regression.

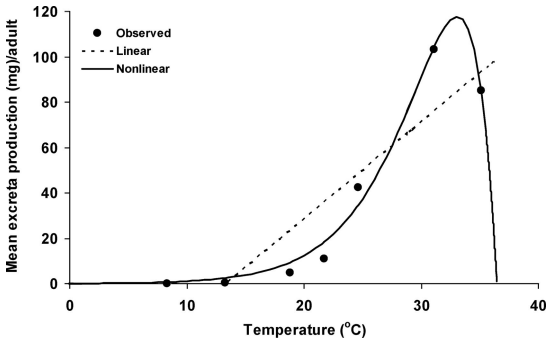

Fig. 3. Temperature-dependent production of xylem excreta (mg) per *H. vitripennis* adult on the lemon plant as fitted to nonlinear Logan model (Logan et al. 1976).

the simulated winter temperatures for Riverside and Oakville, but no excreta production was observed under that of Buntingville, where temperature never surpassed 10°C. Under this regime, notably, 66.7 and 100% of the insects were found inactive on the soil surface at 2- and 9-d exposure, respectively. In contrast, in the other simulated regimes at 9-d exposure, most of the adults (≥80%) remained on the branches.

Repeated measures ANOVA revealed that the numbers of surviving adults were influenced by temperature regime ($F = 29.2$; df = 2, 296; $P < 0.001$) and time ($F = 93.4$, df = 32, $P < 0.001$), with an interaction between regime and time ($F = 15.3$, df = 64, $P < 0.001$) (Fig. 4B). The shape of the mortality curve displayed a nonlinear relationship against exposure time, which was fit to the Weibull equation (equation 1) for each temperature regime to estimate the lethal time at the 10, 50, and 90% mortality levels (Fig. 4B). It is noteworthy that 100% mortality occurred at 14 d when *H. vitripennis* adults were continuously exposed to Buntingville thermal cycles (below 10°C), whereas it took 147 and 161 d to reach 100% mortality under the simulated temperatures of Riverside and Oakville, respectively. The lethal times at 10, 50, and 90% mortality under each simulated temperature were as follows: 12.9, 56.6, and 145.1 d for that of Riverside; 9.3, 44.6, and 145.1 d for that of Oakville; 2.2, 5.3, and 9.1 d for that of Buntingville, respectively.

Cooling Degree-Hours Model. The Weibull model quantified the relationship between CDH and mean mortality ($F = 990.8$; df = 1, 40; $P < 0.001$) and explained 96.2% variability of the data (Fig. 5). The model estimated that 10, 50, and 90% adult mortality would occur at 158.2, 683.2, and 1,736.5 CDH, respectively.

Table 3. Parameter estimates of models to describe the relationship between temperature and hourly excreta production (mg) per *Homalodisca vitripennis* adults

Model	Parameter	Estimate ± SEM	r^2
Nonlinear model	ψ	0.082433 ± 0.333639	0.987
(Logan et al. 1976)	ρ	0.25991 ± 0.54435	
	T_L	36.3938 ± 1.1532	
	ΔT	2.83384 ± 8.20987	
Linear model	a	−57.0764 ± 27.2256	0.731
(Davidson 1944)[a]	b	4.2810 ± 1.2973	

[a] Data range (8.3–31.1°C) chosen for the linear regression.

Validation of the Predictive Model: Field Data. Repeated measures ANOVA revealed a significant difference in the number of surviving adults between Bakersfield and Riverside ($F = 7.04$; df = 1, 233; $P = 0.0173$), time ($F = 144.58$, df = 12, $P < 0.0001$), and interaction of times and site ($F = 6.77$, df = 12, $P < 0.0001$). In Bakersfield, 100% mortality was observed in early January 2007 (3 and 10 January for two different cages), whereas 99.3% mortality was observed in Riverside on 28 February 2007 (Fig. 6). There was a difference in temperature condition between the two field sites and also between the two cages at each site. Accumulated CDH over the entire observation period (29 November 2006–28 February 2007) were 8,341.4 and 7,981.1 CDH at two cages in Bakersfield, whereas they were 4,639.3 and 4,844.7 CDH at two cages in Riverside. The cooling degree-hours model provided a reliable prediction of the temporal pattern of overwintering mortality of *H. vitripennis* adults throughout the monitoring period at both sites, estimating that time of 90% mortality would occur on 19 December and 20 December for the two Bakersfield cages and 30 December and 31 December for the two Riverside cages (Fig. 6). Over the pooled data, there was no significant difference between the observed and predicted values of mortality (Wilcoxon paired-sample test, $P > 0.05$), although some level of discrepancy was observed particularly in the early period of monitoring (Fig. 6). The deviation of predicted mortality (%) at the dates corresponding to observation ranged from 0 to 28.5%, with <5% mean deviation (4.7 ± 2.6%, mean ± SEM).

Validation of the Predictive Model Using Weather Data. Accumulated CDH throughout winter also varied among years, which resulted in annual variation of the estimated overwintering mortality. The overwintering mortality in Riverside, estimated by the predictive model, showed a yearly variation (over nine winter seasons, 1998–1999-2006–2007) that ranged from 82.2 to 99.0% in the 1999–2000 and 2003–2004 winters, respectively (Table 4). Mean percentage of overwintering mortality indicated that 92% of overwintering *H. vitripennis* adults in Riverside would die before reproduction in spring. In Riverside, Castle et al. (2005) showed that the adult density in untreated lemon trees declined from ≈25 to 1 per sample unit (≈96% mortality) in late October 2001 through late February 2002. Using temperature data from the weather station, our model estimated 98% mortality over the similar corresponding period (1 November 2001–28 February 2002).

Discussion

Regression models in this work quantitatively described the temperature-dependent pattern of *H. vitripennis* feeding in terms of both xylem excreta and the percentage of adults producing excreta by applying the models of Logan et al. (1976) and Weibull (Cock-

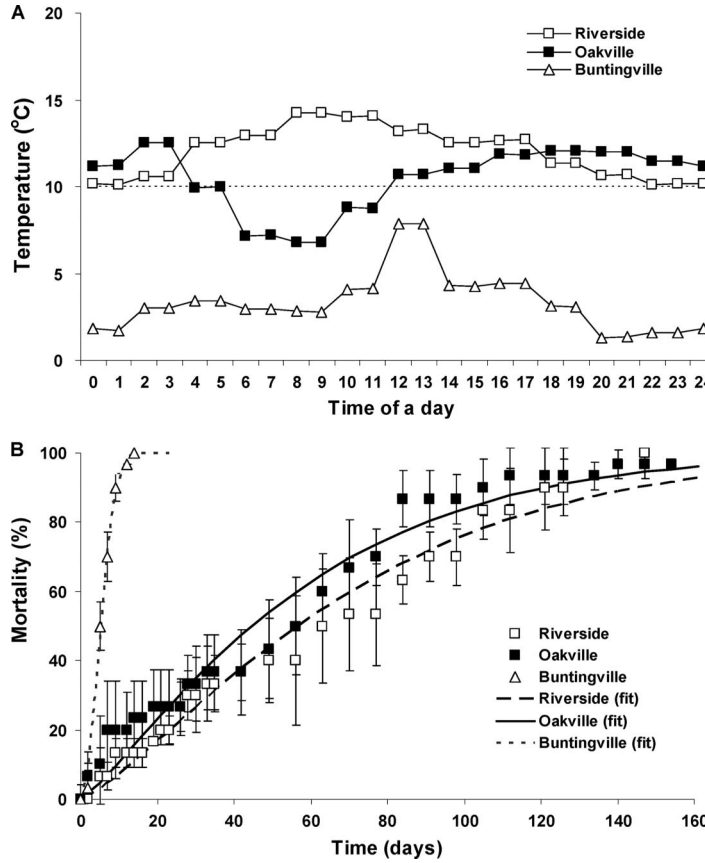

Fig. 4. Mortality under simulated winter temperatures at three locations in California: (A) actual hourly thermal profile to which the *H. vitripennis* adults were exposed and (B) percent mortality (mean ± SEM) fitted to Weibull equation for each treatment.

field et al. 1994), respectively. We found that temperature-dependent excreta production showed the typical nonlinear pattern commonly found in insect development, which is why the Logan model fit the pattern. The estimated upper threshold temperature (36.4°C) indicated that *H. vitripennis* feeding activity would be severely inhibited because of insect physiological stress at temperatures equal or higher than the threshold. In fact, no adults tested in our study survived the 48-h trial at 40.8°C. Similarly, we have ob-

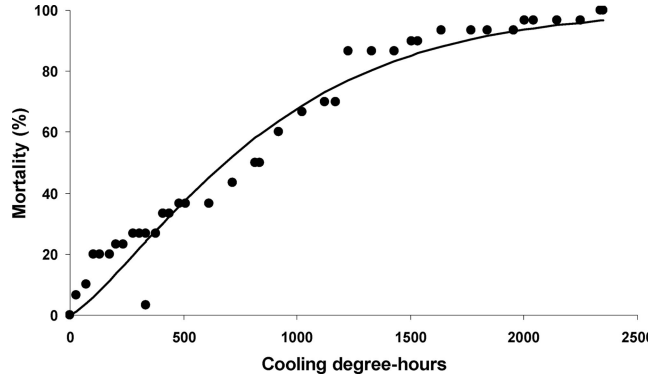

Fig. 5. Cooling degree-hours model to describe the temperature-dependent percent mortality of *H. vitripennis* adults using the Weibull equation Parameter estimates (±SEM) to describe the relationship between cooling degree-hours and the percent mortality of *H. vitripennis* obtained from simulated temperature experiment were $\alpha = 908.323 \pm 31.152$ and $\beta = 1.286 \pm 0.075$ ($r^2 = 0.962$).

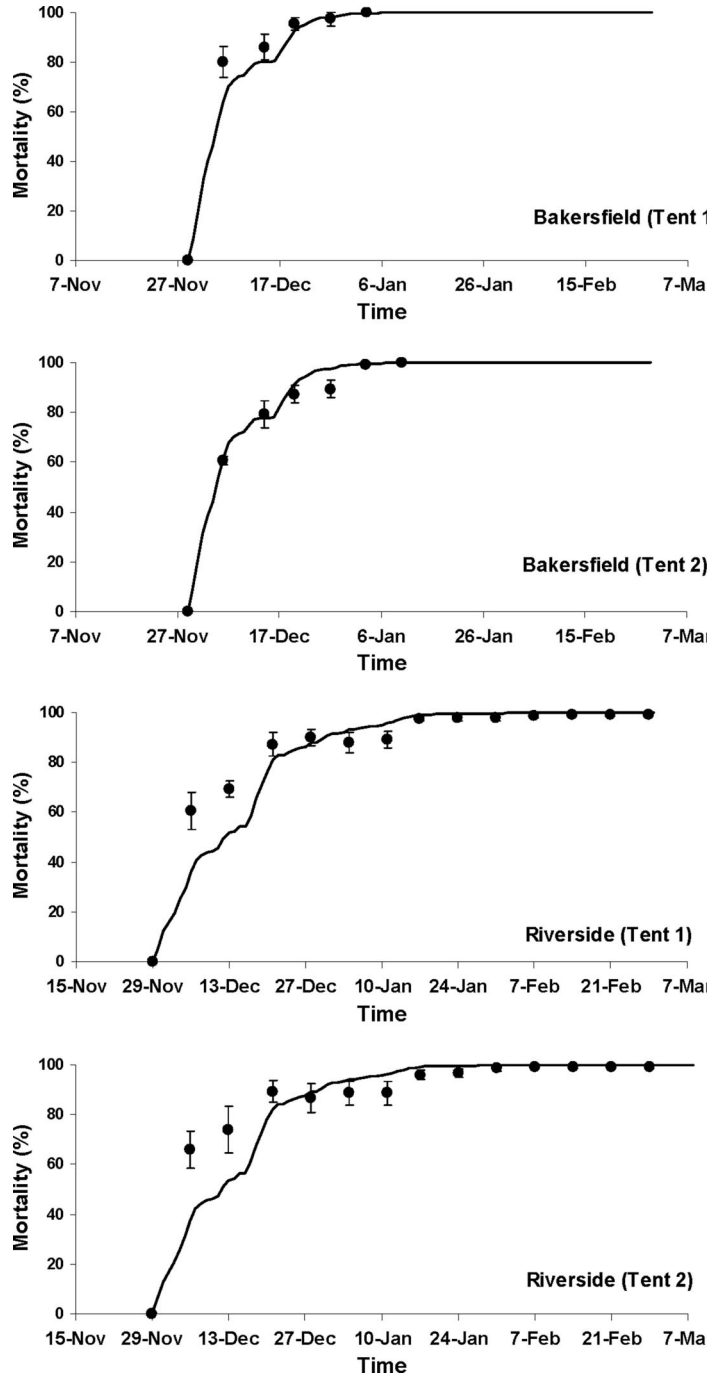

Fig. 6. Comparison of percent mortality of *H. vitripennis* adults predicted by the cooling degree-hours model with those adults observed in field cages in Bakersfield and Riverside. Four sets of data (two for each site) were used to validate the model.

served that *H. vitripennis* adult longevity was negatively influenced by continuous exposure to high temperatures (Son et al. 2009). However, unlike the adults we confined in the sachet, adults in the field might be capable of actively avoiding unfavorable microclimates upon exposure to the extreme conditions, as a result of thermoregulatory behavior. As a result of the relative large volume of xylem sap passing through the digestive system in a short period, these insects also may be able to regulate body temperature according to feeding substrate versus ambient temperature. Note that under field conditions, plants are

Table 4. Estimated overwintering mortality of *Homalodisca vitripennis* in Riverside against CDH using weather station data

Winter season	CDH[a]	Mortality (%)
1998–1999	1,524.8	85.7
1999–2000	1,387.5	82.2
2000–2001	2,831.7	98.7
2001–2002	2,631.8	98.0
2002–2003	1,477.5	84.6
2003–2004	2,959.7	99.0
2004–2005	1,992.3	93.6
2005–2006	1,662.3	88.7
2006–2007	2,568.1	97.8
Mean ± SEM	2,115.0 ± 210.9	92.0 ± 2.3

[a] Cooling degree-hours for each overwintering year, calculated using hourly ambient temperature data obtained from Riverside weather station, were accumulated from Nov. through Feb.

able to reduce leaf surface temperature by increasing transpiration (i.e., opening stomata). In our study, whole plants were kept in temperature cabinets, which equalized food and ambient temperatures. Additionally, duration of exposure to such extreme temperatures would be relatively short under fluctuating field temperatures. Nonetheless, it is evident that *H. vitripennis* feeding was significantly influenced by temperature because all tested adults fed at ≥24.6°C.

In the linear regression analysis, the estimated lower threshold (13.3°C), based on the hourly excreta amount, was higher than that of 10.0°C, which was based on the percentage of adults producing excreta. The value 10.0°C appeared to be more appropriate for two reasons, as follows: 1) one adult was still capable of feeding at 13.3°C, and 2) the pattern of excreta production was poorly explained by the linear model (r^2 = 0.731), which displayed a typical nonlinear shape than that of the percentage of adults with excretion (r^2 = 0.938). Thus, the lower threshold (10.0°C) estimated from the linear regression on the feeding frequency was more reasonable.

Little attention has been focused on how *H. vitripennis* feeding is affected by abiotic environmental factors. In contrast, the impacts of host plant characteristics (e.g., nutrient composition, plant species, and xylem tension) have been well studied (Andersen et al. 1992; Brodbeck et al. 1993, 1995, 2004). Increased xylem tension within a nonirrigated host plant negatively influenced feeding (in terms of excreta production) of *H. vitripennis* adults (Andersen et al. 1992). Feeding rates of the adults were correlated with the diurnal cycles in xylem fluid chemistry, such as the ratio of nutrients (i.e., ratio of amides to total organic compounds) (Andersen et al. 1992) or the concentration of nutrients (i.e., total amino acid concentration) (Brodbeck et al. 1993). The findings in this study imply that effects of these plant variables on the insect's feeding could be more evident when the insects are able to feed under conditions where the ambient temperature stays near optimal or at least above the threshold. At low temperatures (≤7.8°C) below the threshold, independent of host plant availability, the insects were physiologically inactive without any feeding or movement (Son et al. 2009). Under field situations, if temperature stays above the threshold long enough to trigger activity of this insect, plant characteristics can be more influential on host selection behavior, particularly host acceptance and use (Bi et al. 2005, Nadel et al. 2008, Krugner et al. 2009).

In addition to those plant variables reported in previous studies, this study clearly demonstrates that adult feeding rate is highly dependent upon feeding substrate and ambient temperatures. We showed that the amount of xylem excreta per adult increased by 207-fold when temperature increased from 13.3 to 31.1°C (Table 1). Results from our simulated temperature experiment indicated that prolonged exposure to moderately cold temperatures (below the threshold, but above 0°C) increases mortality apparently because of starvation. For instance, 100% mortality occurred in 2 wk at the regime of 1.3–7.9°C versus 21 wk at the regime of 10.1–14.4°C. Consistent with a previous field observation (Pollard and Kaloostian 1961), *H. vitripennis* adults maintained at thermal cycles continuously below the threshold dropped onto the soil surface. The similarity in *H. vitripennis* survival recorded from the simulated temperature regimes for Riverside and Oakville suggests that the insect may obtain adequate resources to survive over winter as long as the temperature cycles remain above the lower threshold for a certain period of time even when winter feeding is restricted to relatively short periods. Nonetheless, the longevity of the sharpshooters under both winter-simulated conditions was much shorter, compared with those (100% mortality at 36 wk) kept under constant 23.4°C in the previous study (Son et al. 2009).

By linking temperature cycles, feeding activity, and survival rates, the model based on the lower threshold required for feeding explained 96.2% of the variance associated with *H. vitripennis* survivorship, thereby supporting our finding that starvation resulting from insect inactivity during the cold period is a critical factor affecting mortality. The period of inactivity caused by low temperatures as measured in terms of cooling degree-hours was a reliable predictor of overwintering mortality in *H. vitripennis* adults. Previous studies indicated that *H. vitripennis* adults overwinter in some areas of California, and they flew under warm conditions during the winter, based on the number of adults captured on yellow panel traps (Park et al. 2006). As a winter-active species, *H. vitripennis* adults would be more directly influenced by increases in winter temperatures than winter-inactive species (in a diapausing status) because of enhanced feeding and consequential reduced chances of mortality (Battisti et al. 2005). For winter-active species, winter warming appeared to be responsible for range expansion (to higher latitudes and elevations), for example, as observed in the lepidopterans *Atalopedes campestris* (Boisduval) (Crozier 2003) and *Thaumetopoea pityocampa* (Denis and Schiffermüller) (Battisti et al. 2005), and coleopteran *Dendroctonus frontalis* Zimmermann (Williams and Liebhold 2002). Therefore, as in these species, winter warming caused by climate

change may allow *H. vitripennis* to colonize beyond its current distribution by increasing the overwintering success, which may further result in changes in the risk of Pierce's disease epidemics and other diseases caused by *X. fastidiosa.*

The cooling degree-hours model was a reliable predictor to describe the temporal pattern of overwintering mortality of *H. vitripennis* under field conditions in Bakersfield and Riverside. The model somewhat underestimated the mortality in the early weeks after field release, which seemingly resulted from insect stress before field release (i.e., collection, aspiration, and transportation). Although the field-cage study confirmed our laboratory results, extrapolation of findings from the field-confinement experiment to an open-field situation should be done with caution for several reasons. First, the microclimate inside the field cages appeared to be cooler than that in the open field, and this was the result of double screening of direct sunlight. Second, the adults confined within the cage had limited access to more favorable host plants. In a field situation, they may be capable of dispersing and actively seeking better host plants (Blua and Morgan 2003, Bi et al. 2005, Krugner et al. 2009). Third, removal of plant litter on the soil surface in this study eliminated shelter that potentially might have mitigated direct chilling injury or cold shock during winter nights (Leather et al. 1993). In the field, low vegetation cover and plant litter often exist on the ground where *H. vitripennis* adults drop during cold periods.

Temperature data acquired from a local weather station were used in the model to estimate overwintering mortality of *H. vitripennis.* Results estimated that an average of 8% of the *H. vitripennis* adults in Riverside would be able to survive and reproduce in spring, although annual variation of overwintering mortality existed because of yearly differences in winter temperatures. These results indicate that the model would also estimate winter mortality of *H. vitripennis* populations at multiple geographical locations where winter climate condition varies, which would be useful to compare the overwintering success among locations. By using cooling-degree days based on the feeding threshold of 10°C and temperature data from weather stations, Johnson et al. (2008) developed geographic information system mapping of postwinter mortality of *H. vitripennis* adults and showed that the mortality in most winters would range 80–90% in most agricultural areas of the Central Valley. The prediction results estimated by using weather-station temperature data have yet to be validated, possibly because of the difference in temperature data between the weather station and the actual microhabitat where this species actively disperses over winter (Blua and Morgan 2003, Park et al. 2006), although both temperatures tend to be closely correlated (Lam and Pedigo 2000).

The predictive model in this study allowed the estimation of the survival of overwintered adults by accumulating cooling degree-hours throughout winter. If one knows the density of *H. vitripennis* adults entering the overwintering period, the relative density of the following early spring population can be estimated (Bale 1991). Therefore, population dynamics during late summer and early fall periods must be integrated to provide a complete picture on the survival potential of *H. vitripennis.* In summary, our study clearly demonstrated that the feeding activity of *H. vitripennis* adults is strongly influenced by temperature. The predictive model described in this work has good potential to predict the temporal and spatial pattern of overwintering success for *H. vitripennis* adults based on current annual temperature profiles.

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