Influences of Temperature on *Homalodisca vitripennis* (Hemiptera: Cicadellidae) Survival Under Various Feeding Conditions

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ABSTRACT Survival of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), was studied under various constant temperatures and feeding conditions. When provided a host plant (*Citrus limon* L. Burm. f.) to feed on during a 21-d trial, 100% mortality occurred at 0.1, 3.2, and 40.1°C, whereas an average of 74–76% of adults survived in the 13.2–24.5°C range. When individually confined with moist cotton, adult longevity was greatest (16.3 d) at 13.3°C, but it was <3 d at −2.4 and 36.2°C. In a companion study comparing the presence versus absence of a host plant, the presence of a host plant was not a significant factor influencing survival at temperatures ≤7.8°C but was at temperatures ≥18.9°C. The relationship between temperature and survival was described by a nonlinear function that estimated the optimum temperature in each feeding regimen: no host plant or moist cotton (5.5°C), moist cotton (9.9°C), and accessible host plant (25.1°C). The model quantitatively predicted that *H. vitripennis* would survive longer periods at a wider temperature regimen when provided with a host plant than when provided with water alone (moist cotton) or when provided with neither plant host nor water. Our results suggest that continuous exposure to either low (<5°C) or high (>30°C) temperatures are detrimental for adult survival. Specifically, low temperatures caused early mortality because of inhibition of feeding activity and presumably this threshold lies between 7.8 and 13.2°C. Furthermore, this study clearly shows that temperature may influence the survival of *H. vitripennis* adults regardless of feeding regimens, and its implications for population dynamics are discussed.

KEY WORDS glassy-winged sharpshooter, Cicadellidae, survival, temperature, feeding, vector

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), is indigenous to the southeastern United States and northeastern Mexico (Turner and Pollard 1959, Triapitsyn and Phillips 2000, Takiya et al. 2006) and was initially detected in California in 1989 (Sorensen and Gill 1996). Since then, *H. vitripennis* populations have established throughout portions of southern California and the southern San Joaquin Valley (Blua et al. 1999, 2001). Incipient populations were detected occasionally as far north as Sacramento and Butte Counties (CDFA 2003). This xylem-feeding insect has a wide host range of >100 plant species in 31 families (Adlerz 1980, Hoddle et al. 2003). While feeding, *H. vitripennis* may transmit the pathogenic bacterium *Xylella fastidiosa*, resulting in the destructive Pierce's disease (PD) of grapevines as well as other scorch-like diseases in various agricultural and landscape plants (Blua et al. 1999, Hopkins and Purcell 2002).

The bacterium *X. fastidiosa* and several native leafhopper vectors have been present in California for >100 yr (Purcell 1977), and PD outbreaks have occurred periodically in coastal vineyards and in vineyards in the San Joaquin Valley (Varela et al. 2001, Redak et al. 2004). However, recent increase of PD in southern California vineyards (i.e., Temecula in 1990s) has been attributed to the invasion and establishment of *H. vitripennis*, a known vector of *X. fastidiosa* (Purcell and Saunders 1999, Almeida and Purcell 2003, Blua and Morgan 2003). In comparison with native vector species, *H. vitripennis* disperses farther into vineyards (Burks and Redak 2003, Blackmer et al. 2004) and is capable of transmitting *X. fastidiosa* secondarily or vectoring vine-to-vine (Varela et al. 2001). Continuous expansion of *H. vitripennis* in California poses severe threats to agricultural industries, including its $ 3.2 billion-valued grape and $897 million-valued almond industry (CDFA 2003). Areawide control measures have been implemented throughout California to suppress and prevent further spread us-

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ing a combination of insecticide treatments, biological controls, and quarantine measures (CDFA 2005).

Further spread and establishment of this invasive species may depend on climatic conditions in noncolonized locations (Tauber et al. 1986, Javis and Baker 2001). The native range of *H. vitripennis* coincides with the tropical and subtropical zones (Turner and Pollard 1959, Triapitsyn and Phillips 2000, Almeida and Purcell 2003), where climatic conditions also appear favorable for *X. fastidiosa* overwintering and persistence through mild winters (Purcell 1977). Feil and Purcell (2001) reported that low temperatures (≤12–17°C) adversely influenced the growth and survival of *X. fastidiosa.* Similarly, populations of *H. vitripennis* in the southeastern United States and California are likely to be constrained by climatic factors that limit the pest's establishment and persistence (Hoddle 2004). This species overwinters as adults (Turner and Pollard 1959), and during that period, a majority of the females seem to be reproductively inactive (Hummel et al. 2006). During winter, however, the adults feed and fly during warm conditions (Pollard and Kaloostian 1961, Blua and Morgan 2003, Almeida et al. 2005, Park et al. 2006). Therefore, if feeding of *H. vitripennis* adults is influenced by temperature conditions, the prevailing low winter temperatures of specific areas in northern and central California may limit feeding activity, which would further increase overwintering mortality. Because a single *H. vitripennis* female can potentially oviposit 500–1,100 eggs (Leopold et al. 2004), colonization of *H. vitripennis* is likely to be highly dependent on the numbers of overwintering adults that survive to reproduce in spring. In nonmanaged areas, *H. vitripennis* adults exist in high densities in California's southern and coastal citrus orchards, which are considered a major reservoir for overwintering *H. vitripennis* in some regions (Perring et al. 2001, Grafton-Cardwell et al. 2003). The discrete citrus-growing zone in the southern San Joaquin Valley of California (along the eastern side of the valley at the base of the Sierra Nevada Range) experiences relatively mild winter climates, where increases in *H. vitripennis* populations and PD incidence have been concomitantly reported in 2000–2001 (Grafton-Cardwell et al. 2003).

Few published studies exist on the influences of temperature on the seasonal biology of *H. vitripennis,* which is fundamental to understanding insect population dynamics and managing populations (Danks 1994). Pollard and Kaloostian (1961) observed that overwintering *H. vitripennis* adults generally remained sessile at temperatures <9.4°C, and first flights occurred only after the ambient air temperature had exceeded 11°C. In a laboratory study, xylem excreta production by adult *H. vitripennis* was heavily curtailed at low temperatures (≤13.3°C) (Johnson et al. 2006). These results support the hypothesis that *H. vitripennis* feeding is highly influenced by temperature condition of the surrounding environment. At 27°C, mortality of *H. vitripennis* adult females was >60% after 68 d and >95% after 133 d when reared on cowpea plants (Setamou and Jones 2005). Eggs of *H. vitripennis* completed development at 16.7–35°C and required 113.8 DD to hatch with a lower threshold of 11.9°C (Al-Wahaibi and Morse 2003).

In southern California, field studies suggest that *H. vitripennis* produces two generations per year (Blua et al. 1999, 2001; Castle et al. 2005), as in its native range of the southeastern United States (Turner and Pollard 1959). Castle et al. (2005) reported that adult densities gradually decreased through the winter into the following spring. As such, to our best knowledge, there is no published data to determine the impact of temperature on *H. vitripennis* adult survival. Such information would contribute to the effective design of mass-rearing systems and experimental protocols, implementation of effective pest management programs by predicting the annual phenology of *H. vitripennis,* and delineation of the potential geographical range of *H. vitripennis* by estimating the chances of overwintering success based on climate data.

This is the first study to investigate the effects of temperature on *H. vitripennis* adult survival. The objectives of this study were to (1) determine the effects of various temperatures on *H. vitripennis* adult survival when maintained under different feeding conditions and (2) describe the survival pattern of *H. vitripennis* in relation to the combination of these two factors by applying empirical models.

Materials and Methods

Insect Colony. Because of quarantine restrictions limiting the possession of live *H. vitripennis* within specific areas of the San Joaquin Valley in California, all laboratory studies were conducted in a contained, restricted-access laboratory established on the campus of California State University at Fresno (CSUF). Insects used in experiments were laboratory-reared, young adults (<3 wk old), which were initially obtained from the rearing facility at the California Department of Food Agriculture (CDFA) Field Station, Arvin, CA. At the CDFA rearing facility, the laboratory colonies of *H. vitripennis* were reared from egg stage on multiple host plants under greenhouse conditions at 31 ± 4°C and a photoperiod of 16:8 (L:D) h. On transfer, the adults were maintained in screened rearing cages containing potted plants of cowpea (*Vigna unguiculata* L. Walp.) and 'Frost Eureka' lemon (*Citrus limon* L. Burm. f.) at the CSUF facility.

Constant Temperature Studies. Experiments were conducted to determine the effects of constant temperatures on *H. vitripennis* adult survival for various exposure intervals under three different feeding regimens: (1) access to host plant, (2) water only, and (3) no water or host plant. Lemon tree (*C. limon* Frost Eureka) was chosen as the host plant, because citrus is one of the most important hosts for *H. vitripennis* breeding and overwintering in California (Grafton-Cardwell et al. 2003, Bi et al. 2005, Castle et al. 2005), and proximity to citrus groves has influenced the incidence and severity of PD in vineyards (Perring et al. 2001). The cultivar Frost Eureka used in this study was tolerant of the temperature regimens in our prelimi-

nary trials and is one of the most common commercial cultivars (Irvin and Hoddle 2004). All measurements were made in environmental chambers under 60–80% RH and a photoperiod of 10:14 (L:D) h. Actual temperatures inside each chamber were monitored using a data logger (HOBO; Onset Computer, Bourne, MA) and used as a treatment factor in each trial. All the experiments were conducted from 1 February 2005 through 7 April 2006.

Survival When Provided Host Plant. This study quantified the effects of temperature and sex on survival of *H. vitripennis* adults when provided continuous access to a potted (3.8-liter pot) lemon plant as a feeding host. A cage, similar to that of Setamou and Jones (2005), was used to enclose the adults and the plant. The cage (70 cm height, 15 cm diameter), with a screened sleeve on top and two screened ventilation holes (2.5 cm diameter) on its wall, was installed by overtopping the potted plant. Ten adults of each sex were separately placed into the cage, which was transferred to one of the environmental chambers maintained at constant temperatures of 0.1, 3.2, 6.2, 13.2, 18.7, 24.5, and 40.1 ± 1.0°C. A group of 10 insects was considered a replicate, and each treatment had a minimum of four replicates per sex. The number of surviving adults was monitored every 1–7 d up to 21 d after exposure.

Longevity When Provided Water Only. This experiment quantified temperature effects on adult longevity of *H. vitripennis* males and females when no suitable feeding host was present, and adults had access to water only. This experiment was conducted to identify potential compounding impacts of host plant physiology or quality on adult survivorship at different temperatures. Adults were sexed and individually transferred to a clear plastic tube (33 ml; Bioquip Products, Rancho Dominguez, CA) provisioned with moist cotton, with two ventilation holes (2 mm diameter). During this test, the cotton was kept moist by replenishing water until saturation if it was dry at each observation time. The tubes were randomly assigned to the environmental chambers, of which the constant temperatures were −2.4, 5.0, 8.6, 12.9, 19.0, 21.3, 24.8, and 36.2 ± 1.0°C. Numbers of surviving adults were counted daily until all test insects died in each treatment. An individual insect was considered a replicate, and each treatment had a minimum of 20 replicates per sex.

Survival With and Without a Feeding Host. In the first test, we observed rapid mortality at low temperatures without production of any xylem excreta. Therefore, we hypothesized that a lack of feeding at low temperatures would be a major mortality factor. This trial was conducted to determine whether the presence of a host plant was a critical factor at specific temperatures, with a reasonable expectation that adult survivorship would be similar in the presence or absence of a feeding host at temperatures below which feeding does not occur. Because survival of *H. vitripennis* adults was not significantly different between sexes in the two previous tests, adult sex was not distinguished for this test. On capturing the adults from rearing cages, 10 adults were placed into an experimental cage (as described above) attached to a pot containing either a lemon plant or no plant. Cages were randomly assigned to environmental chambers held at the following constant temperatures: −2.1, 2.5, 7.8, 18.9, 23.4, and 34.9 ± 1.0°C. The 10 adults in a cage were considered a replicate, and each temperature treatment had three replicates. The number of surviving adults was monitored every 1–7 d until 100% mortality occurred in all replicates.

Data Analysis. In the first and third tests, adult survival (%) as a response variable was transformed by arsine-square root before the statistical analysis. Kaplan-Meier survival analysis (Kaplan and Meier 1958) was performed to compare the survivorship patterns among temperatures. Longevity data as a response variable in the second study were checked for normality and were subjected to square-root transformation to achieve a normal distribution. The presence of a treatment effect was determined using analysis of variance (ANOVA) at the 5% significance level (SAS Institute 1998). Means were separated by Tukey's honestly significant difference (HSD) test. For all studies, treatment means ± SEM are presented unless otherwise noted.

Model Development. Quantitative models were developed to describe the survivorship patterns of *H. vitripennis* adults relative to temperature and exposure duration for each feeding regimen (i.e., host plant, water only, no water or host plant). Data collected from the constant temperature experiments were categorized depending on feeding regimen, in which data were pooled regardless of sex at each temperature and calculated as survival (%) against time. Estimates of regression model parameters were obtained using the TableCurve 2D Program (Jandel Scientific 1996).

Survivorship Curves. To estimate exposure time to 50% mortality (LT_{50}), the survivorship curve at each temperature was described by using the Weibull model (Madden et al. 1984):

$$S(t) = \exp[-(t/\alpha)^{\beta}] \quad [1]$$

where $S(t)$ is the probability that an insect lives at least to time t (in d), α is a scalar parameter that is inversely related to the mortality rate, and β is a shape parameter that allows the model to present survival distributions. The percentage of live adults (survival) was calculated by dividing the number of live adults at each exposure time by the initial number of adults tested. From the model obtained, LT_{50} was estimated at each temperature for each feeding regimen.

Survivorship curves within each feeding regimen showed very similar shapes, irrespective of temperature difference. To describe temperature-independent survivorship for each feeding regimen, the Weibull model was applied by fitting survival data (pooled from all temperatures) against normalized time (Wagner et al. 1984). Before data fitting, exposure times at each temperature were normalized by dividing the exposure time by the estimated LT_{50}, and the survival data were plotted against the normalized time.

Temperature-Dependent Model. At each feeding regimen, the relationship between the time to the 50% mortality (LT_{50}) and temperature (°C) was fitted to the nonlinear, extreme value model (Kim and Lee 2003):

$$LT_{50}(T) = k \exp[1 + (T_{max} - T)/\rho - e^{(Tmax - T)/\rho}] \quad [2]$$

where $LT_{50}(T)$ is the time to 50% mortality at temperature T (°C), k is the longest time to reach 50% mortality, T_{max} is the temperature (°C) at which the longest time to 50% mortality occurs, and ρ is a fitted parameter. The values of LT_{50} used as dependent variables in this analysis were obtained from the Weibull model (equation 1).

Simulation Model. Integration of the distribution model and temperature-dependent model has been used to simulate insect phenology through time at constant temperature (Wagner et al. 1985, Allen et al. 1995). Using a similar protocol, we constructed a simulation model to predict survival of *H. vitripennis* adults in relation to exposure time (t) and temperature (T) by combining the survivorship curve model (equation 1) and the temperature-dependent model (equation 2) under each feeding condition. Parameter estimates for these two models were different among feeding regimens, which were obtained from regression analyses above and used for this simulation. Similar to insect development simulation (Wagner et al. 1985, Allen et al. 1995), the temperature-dependent model determines time to 50% mortality (LT_{50}) at a given temperature, and the survivorship curve model determines survival distribution at a given time. The mathematical expression of the simulation model is:

$$F(t,T) = \exp\{-[t/\alpha LT_{50}(T)]^{\beta}\} \quad [3]$$

where $F(t,T)$ is the survival (%) of the insects at constant temperature T at time t, $LT_{50}(T)$ is the temperature-dependent model for time to 50% mortality; and α and β are fitted parameters from the survivorship curve against normalized time.

Results

Constant Temperature Studies

Survival When Provided Host Plant. Repeated-measures ANOVA showed that survival of *H. vitripennis* adults was influenced by temperature ($F = 70.93$; df = 6; $P < 0.001$) and exposure time ($F = 133.03$; df = 5; $P < 0.001$), with an interaction between time and treatment ($F = 8.94$; df = 30; $P < 0.001$; Fig. 1). However, there was no significant effect of sex at any observation time ($P > 0.05$). Kaplan-Meier survival analysis using pooled data of males and females also showed that there were differences in *H. vitripennis* survival rates among temperature treatments ($\chi^2 = 674.34$; df = 6; $P < 0.0001$). Adult survival decreased dramatically at low temperatures (≤6.2°C), whereas survival from 13.2 to 24.5°C remained higher than 68% in the 21–d trial. At the end of the trial, all adults held at the temperature extremes (0.1, 3.2, and 40.1°C) were dead; these data were included to estimate the time to 50% mortality for modeling analysis. Notably, 100% mortality occurred in 7 d at 0.1°C. Production of xylem excreta (as an indicator of feeding) by adults was observed only at temperatures ≥13.2°C. At temperatures ≤6.2°C, adults were often found on the soil surface instead of the plant stems or leaves (another indication that feeding did not occur).

Longevity When Provided Moist Cotton Only. Adult longevity was influenced by temperature ($F = 21.12$; df = 7, 324; $P < 0.001$), but there was no effect relative to sex ($F = 0.37$; df = 1, 324; $P > 0.05$) or interaction between sex and temperature ($F = 1.72$; df = 7; $P > 0.05$; Table 1). Because no difference existed between sexes, data from both sexes were pooled to compare the means among temperature treatments (Table 1). The greatest longevity (16.3 ± 1.8 d) occurred at 12.9°C, whereas the mean longevity was <3 d at the low and high temperatures (1.5 ± 0.1 and 2.5 ± 0.3 d at −2.4 and 36.2°C, respectively). The range in individual longevity was 54 (at 8.6°C) to 1 d (at 40.1°C). Survival rates (adult males and females combined) were significantly different among constant temperatures ($\chi^2 = 239.70$; df = 7; $P < 0.001$; Kaplan-Meier survival analysis; Fig. 2).

Adult Survivorship With and Without a Feeding Host. Repeated-measures ANOVA showed that adult survival (%) differed when host plants were present versus when they were absent at 18.9 ($F = 61.81$; df = 1; $P < 0.0014$), 23.4 ($F = 133.31$; df = 1; $P < 0.0003$), and 34.9°C ($F = 94.12$; df = 1; $P < 0.0001$). However, there were no significant effects of treatment at −2.1 ($F = 0.32$; df = 1; $P > 0.05$), 2.5 ($F = 0.40$; df = 1; $P > 0.05$), and 7.8°C ($F = 1.16$; df = 1; $P > 0.05$; Fig. 3). In all treatments, there was a significant effect of exposure time on survival ($P < 0.0001$). Kaplan-Meier survival analysis also indicated that significant differences in *H. vitripennis* survival rates existed between the two treatments at 18.9, 23.4, and 34.9°C ($P < 0.0001$), whereas there was no differences in survival rates between the two treatments at temperatures ≤7.8°C ($P > 0.05$; Table 2). Independent of host availability, 100% mortality occurred in 3, 21, and 24 d at −2.1, 2.5, and 7.8°C, respectively. Notably, the availability of a host plant for feeding was a highly critical factor for survival at temperatures ≥18.9°C. When held without a host plant, 100% mortality occurred in 7, 3, and 2 d at 18.9, 23.4, and 34.9°C, respectively. With a host plant, the highest mean longevity (80.2 ± 2.0 d) occurred at 23.4°C, where one individual survived up to 255 d.

Model Development

Survivorship Curves. Times to 50% mortality (LT_{50}) of *H. vitripennis* adults were estimated for each temperature under different feeding regimens: provisioned with moist cotton (Table 1) and presence versus absence of a host plant (Table 2). Data at 0.1, 3.2, 6.2, and 40.1°C for individuals with a host plant from the first experiment were included to estimate the LT_{50}, which were 0.8, 10.2, 11.0, and 4.2 d, respectively.

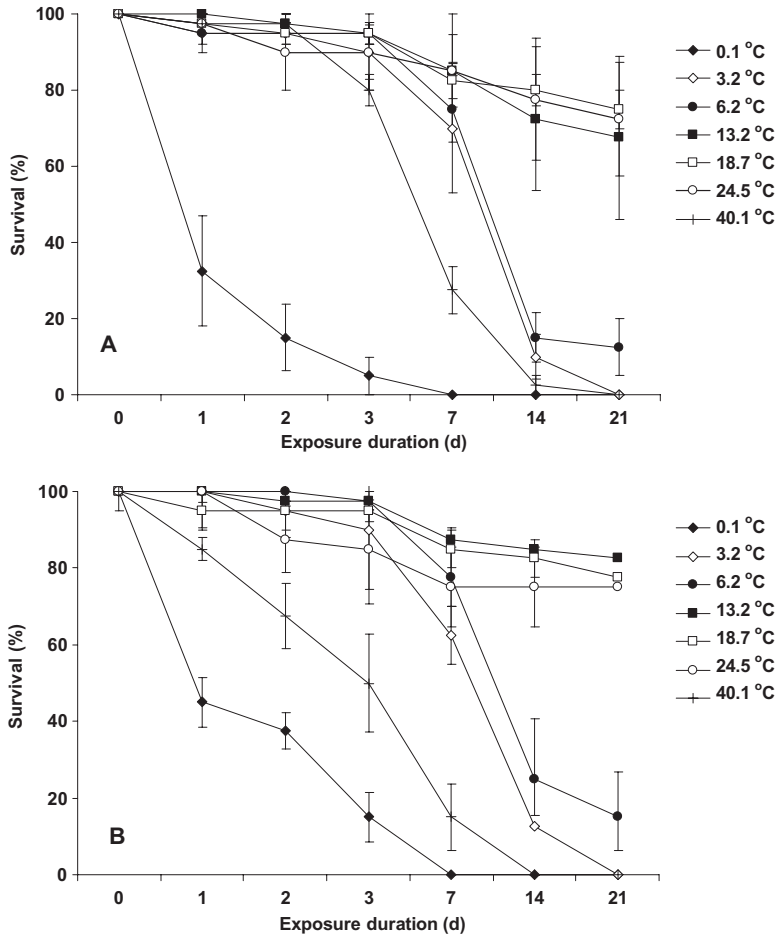

Fig. 1. Percent survival (mean ± SEM) of *H. vitripennis* adults at constant temperatures (°C) when provided a host plant (Frost Eureka lemon) to feed on (A) male and (B) female.

These data were further integrated to develop a temperature-dependent model for a host-feeding situation. Survivorship curves for different feeding conditions were plotted against normalized time (time/LT_{50}; Fig. 4). The shapes of the curves were well described by the Weibull model (Table 3): for no host plant or water ($F = 1991.35$; df = 1,36; $P < 0.001$; $r^2 = 0.983$); water only ($F = 8217.45$; df = 1,125; $P < 0.001$; $r^2 = 0.985$); and presence of host plant ($F = 3256.87$; df = 1,100; $P < 0.001$; $r^2 = 0.970$).

Table 1. Longevity (d; mean ± SEM) and time to median mortality of *H. vitripennis* adults at constant temperatures when individually confined in a clear plastic tube provisioned with moist cotton

Temperature (°C)	Longevity (d, mean ± SEM)[a]					LT_{50} (d)[b]
	n	Male	*n*	Female	Total	
−2.4	20	1.5 ± 0.2c	20	1.6 ± 0.2c	1.5 ± 0.1d	0.4
5.0	20	13.8 ± 2.3ab	20	9.5 ± 1.3ab	11.7 ± 1.3ab	9.0
8.6	20	15.4 ± 2.3a	20	11.7 ± 2.9ab	13.5 ± 1.8ab	9.5
12.9	20	17.8 ± 2.7a	20	15.0 ± 2.3a	16.4 ± 1.8a	13.1
19.0	21	7.6 ± 1.4bc	20	12.2 ± 2.7ab	9.8 ± 1.5bc	6.0
21.3	22	5.2 ± 1.0c	20	6.9 ± 1.0bc	6.0 ± 0.7cd	3.8
24.8	21	3.4 ± 0.4c	21	5.1 ± 0.9bc	4.3 ± 0.5d	2.8
36.2	20	3.1 ± 0.5c	20	1.9 ± 0.2c	2.5 ± 0.3d	1.5

[a] Means followed by the same letter within a column were not significantly different ($P > 0.05$; the Tukey's HSD test).

[b] LT_{50} (d), time to 50% mortality was estimated by fitting survivorship curve of *H. vitripennis* adults (males and females combined) at each temp to the model (equation 1).

Temperature-Dependent Model. The extreme value model (equation 2) provided a reliable description of the relationship between temperature and LT_{50} over the entire temperature range with a high coefficient of determination for all regimens: for no host plant or water ($F = 19.33$; df = 2,5; $P < 0.02$; $r^2 = 0.928$), water only treatment ($F = 25.53$; df = 2,7; $P < 0.001$; $r^2 = 0.911$), and a presence of host plant ($F = 84.26$; df = 2,9; $P < 0.001$; $r^2 = 0.960$; Table 4). The pattern of curves for all regimens exhibited a skewed bell shape, because of the vulnerability to extreme temperatures (Fig. 5A–C). The highest LT_{50} (parameter k) at the optimum temperature (T_{max}) for each feeding regimen was estimated to be 12.0 d at 5.6°C without a host or

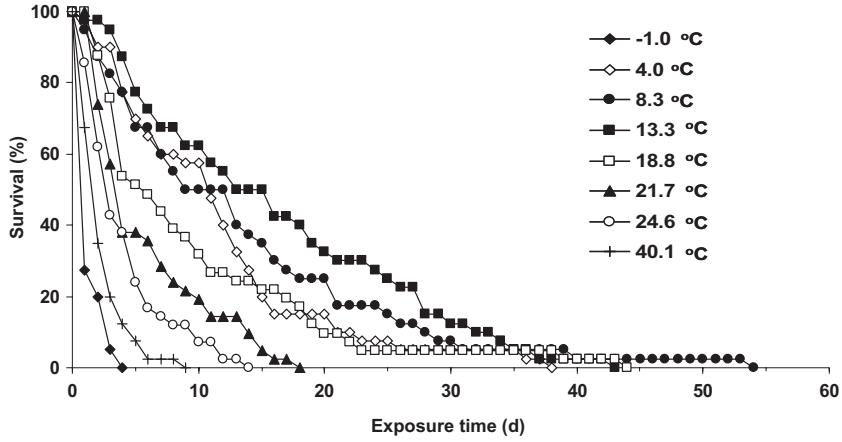

Fig. 2. Survivorship curves of *H. vitripenis* adults (male and females combined) at constant temperatures (°C) when provided with moist cotton.

water, 11.8 d at 10.0°C with water only, and 82.0 d at 25.2°C with a host plant.

Simulation of Survival. The predicted survival of *H. vitripennis* adults in a cohort was presented in relation to temperature and exposure time under different feeding regimens (Fig. 6). Clearly, the results indicate that adults would experience high mortality without water or host plant at high temperatures in comparison with those adults with an available host plant. For instance, when provisioned only with water, 99% *H. vitripennis* adults would die in 10 d at high temperatures (≥28°C), whereas 5% adults would still survive 40 d at 8–13°C (Fig. 6A). When held without host plant or water, 99% of adults would die within 2 d at high temperatures (≥23°C), and only <1% would survive up to 22 d at any optimum temperature (Fig. 6B). With a host plant (Fig. 6C), *H. vitripennis* longevity would greatly increase in comparison with the two previous regimens. More than 20% of adults would survive up to 100 d at 21–29°C, and >2% adults would survive up to 160 d at 22–28°C. At the temperature extremes of ≤5 and ≥36°C, 100% mortality would occur within 36 and 32 d, respectively.

Discussion

This study documented effects of temperature on *H. vitripennis* adult survival under various feeding regimens and provided evidence that adults do not survive under continuous exposure to low temperatures as a result of disrupted feeding. These findings suggest that the overwintering success of this species would be highly dependent on the winter climate. Additionally, winter cold stress unrelated to feeding might also contribute to the mortality of overwintering adults, although cold-hardiness of *H. vitripennis* adults has yet to be studied.

Although few studies on *H. vitripennis* survival exist in relation to temperature, numerous reports show that temperature is one of most important abiotic factors in the biology of other leafhopper species. Leafhopper species found to be susceptible to low temperature exposure include *Circulifer tenellus* (Baker) (Harries and Douglass 1948), *Dalbulus maidis* (Delong and Wolf.) (Davis 1966), *Empoasca fabae* (Harris) (Specker et al. 1990, Sher and Shields 1991), *Erythroneura comes* (Say) (Martinson and Dennehy 1995), and *Macrosteles quadrilineatus* (Stal) (Saini 1967). For instance, low-temperature susceptibility in *E. fabae* was speculated to be an influential factor for seasonal migration (Taylor et al. 1995), phenology (Taylor and Shields 1995), and the overwintering range (Decker and Cunningham 1968, Sidumo et al. 2005). Intriguingly, as observed in *H. vitripennis* herein, *E. fabae* nymphs and adults dropped off plant surfaces when exposed to low temperatures (0–10°C), which was regarded as a low temperature survival strategy (Shields and Sher 1992). High temperature treatments (i.e., 38 and 40°C) reduced *Colladonus montanus* (Van D.) longevity in comparison with individuals held in an unheated control (Jensen 1968). Survival of immature *Empoasca decipiens* Paoli was seriously impaired by high temperatures, where no single egg or nymph completed development at 37.5 and 40°C (Raupach et al. 2002). Al-Wahibi and Morse (2003) reported that at least one *H. vitripennis* egg hatched at 16.7–35°C but none at 11.5 or 40.4°C, and the rate of egg development declined at temperatures higher than 33.4°C. Similarly, our study indicates that high and low extremes of temperatures may negatively influence *H. vitripennis* adult survival.

Survival of *H. vitripennis* adult in relation to temperature and exposure time was graphically shown by applying a series of statistical models for different feeding regimens (see Fig. 2). Overall, nonlinear patterns of survivorship curves suggest that there was variation in survival within *H. vitripennis* adults tested. Such variation in the adults could result from interactions among various factors such as adult age, sex, and nutritional status. Considering that the age of the adults tested was homogeneous and sex was not a significant factor, the nutritional status during the im-

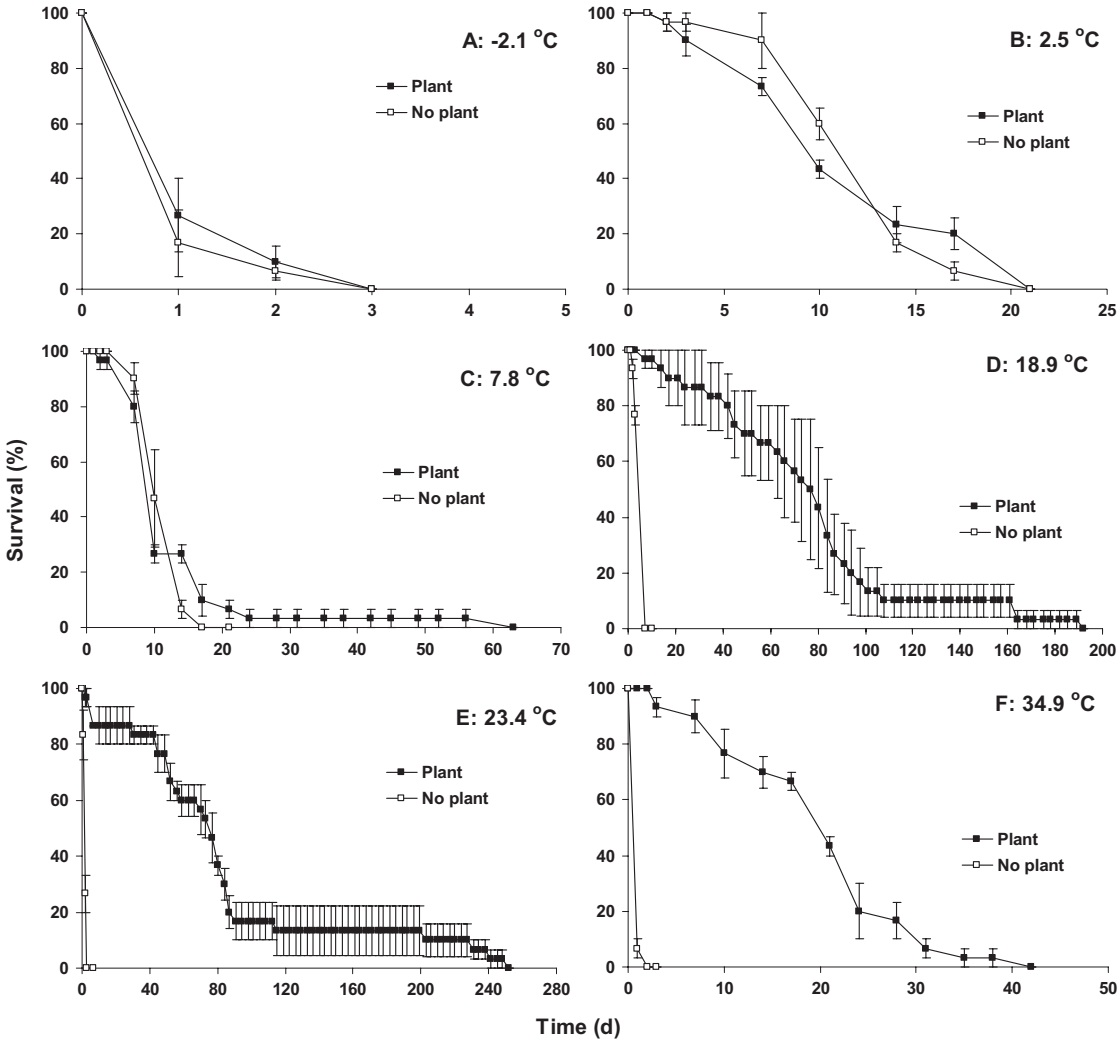

Fig. 3. Survival of *H. vitripennis* adults when held with and without host plant (Frost Eureka lemon) to feed on at constant temperatures: (A): 2.1°C, (B) 2.5°C, (C) 7.8°C, (D) 18.9°C, (E) 23.4°C, and (F) 34.9°C. Water was not provided in either treatment.

Table 2. Estimated longevity (d; mean ± SEM) and time to median mortality (LT_{50}) of *H. vitripennis* adults comparing presence and absence of host plant (Frost Eureka lemon) at constant temperatures

Temperature (°C)	Longevity (d, mean ± SEM)[a]				LT_{50} (d)[b]	
	Host	No host	χ^2	*P*	Host	No host
−2.1	1.3 ± 0.0	1.2 ± 0.0	0.60	0.44	0.5	0.3
2.5	12.0 ± 1.0	12.7 ± 0.1	0.01	0.93	9.9	10.9
7.8	13.0 ± 0.4	11.8 ± 0.1	0.16	0.69	10.8	9.9
18.9	76.0 ± 1.4	5.3 ± 0.0	59.86	<0.0001	70.9	4.0
23.4	80.2 ± 2.0	2.1 ± 0.0	56.67	<0.0001	72.9	1.6
34.9	20.4 ± 0.3	1.1 ± 0.0	64.45	<0.0001	18.9	0.2

[a] Longevity of individual *H. vitripennis* was estimated from the Kaplan-Meier survival analysis.

[b] LT_{50} (d), time to 50% mortality was estimated by fitting survivorship curve to the model (equation 1).

mature stages (often measured by body size or weight) might be one of the most contributing factors to this variation (Scriber and Slansky 1981; Brodbeck et al. 1995, 2004). Nonetheless, the variation was adequately quantified by using the Weibull model in this study, and it is a key component to building realistic life history models (Sharpe et al. 1981, Régnière 1984).

Temperature-dependent survival in terms of the median time of the mortality was fitted to the extreme value function model (see equation 2) (Kim and Lee 2003), which provided the optimum temperature with the longest survival. Clearly, the optimum temperature increased as the adults had access to a water source (10.0°C) or nutrient source (25.2°C), in contrast to that of no access (5.6°C). The width of the suitable temperature range, which is proportional to the absolute value of the shape parameter (ρ), indicates that *H. vitripennis* would survive within a wider

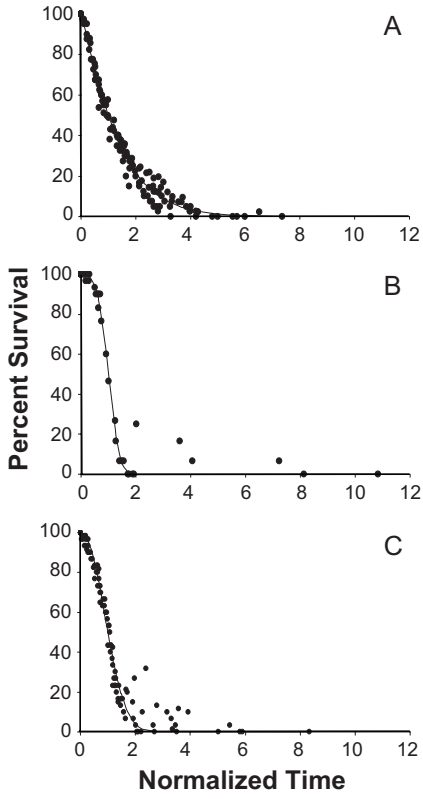

Fig. 4. Observed (●) and predicted survivorship curve (equation 1 of *H. vitripennis* adults against normalized time (time/LT_{50}) when held at different feeding conditions: (A) moist cotton, (B) no water or host plant, and (C) host plant (Frost Eureka lemon).

temperature range when provided a host plant (ρ = 7.0) than with water alone (ρ = 6.6) or neither water nor host plant (ρ = 5.3). Desiccation stress on the *H. vitripennis* adults, because of lack of feeding, seems greater as temperature increased. This phenomenon seems to result from the high feeding rate of xylem-feeding herbivores required to subsist on nutrient-poor food sources composed of >95% water (Raven 1983, Andersen et al. 1989). Unlike the other feeding regimens (Fig. 5A and B), the predicted LT_{50} value of adults with access to a host plant (Fig. 5C) declines more sharply above the optimal temperature than does below the optimal temperature with early mortality observed at those temperatures (34.9 and 40.1°C). Short longevity at those temperatures might also have resulted from the compounding impact of high temperatures on the citrus plant, possibly because continuous exposure to those temperatures might have negatively influenced the plant physiology pertinent to xylem fluid chemistry or tension (Brodbeck et al. 1990, Andersen et al. 1992). By integrating the survivorship curve model and temperature-dependent model of median mortality, the differences in survival of *H. vitripennis* adults under each condition were well described in relation to temperature and exposure time (Fig. 6A–C).

Table 3. Parameter estimates ± SEM of the nonlinear model for survivorship curve (equation 1) against normalized time (time/LT_{50}) under three different conditions

Condition	Parameter	Estimate ± SEM	r^2
Water only	α	1.378 ± 0.016	0.985
	β	1.137 ± 0.024	
No host or water	α	1.115 ± 0.023	0.983
	β	3.564 ± 0.028	
Host	α	1.180 ± 0.016	0.970
	β	2.199 ± 0.099	

Table 4. Parameter estimates ± SEM for the temperature-dependent model (equation 2) of *H. vitripennis* adults against normalized time (time/LT_{50}) to describe a temperature-independent distribution under three different conditions

Condition	Parameter	Estimate ± SEM	r^2
Water only	k	11.843 ± 1.236	0.911
	T_{max}	9.975 ± 0.837	
	ρ	6.590 ± 0.982	
No host or water	k	11.988 ± 1.549	0.928
	T_{max}	5.591 ± 0.939	
	ρ	5.255 ± 0.955	
Host	k	81.752 ± 6.867	0.960
	T_{max}	25.247 ± 0.782	
	ρ	−7.049 ± 0.526	

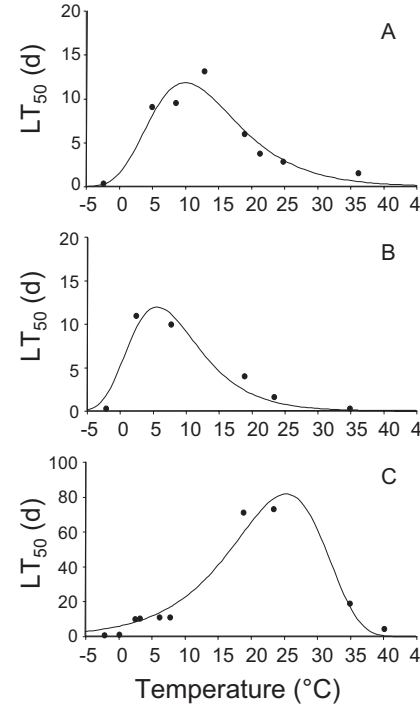

Fig. 5. Observed (●) and predicted time (equation 2) and 50% mortality (LT_{50}) of *H. vitripennis* adults at constant temperatures when held at different feeding conditions: (A) moist cotton, (B) no water or host plant, and (C) host plant (Frost Eureka lemon).

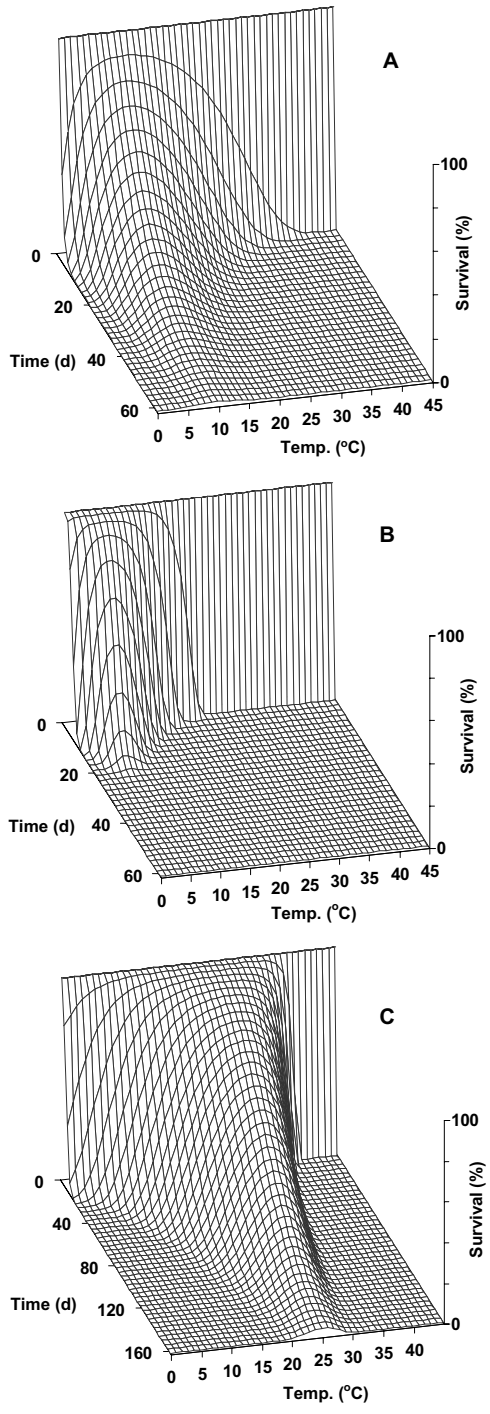

Fig. 6. Simulated density curves (equation 3) of *H. vitripennis* adults survival in relation to constant temperatures (°C) and time (d) when held under different feeding conditions: (A) moist cotton, (B) no water or host plant, and (C) host plant (Frost Eureka lemon).

Survival of *H. vitripennis* varies with host plant species, genotype, and seasonal changes in nutritional quality of the xylem fluid (Andersen and Brodbeck 1989, Brodbeck et al. 2004). Therefore, *H. vitripennis* longevity on different plant species may vary from what we observed, even at the same temperature regimen. Although *H. vitripennis* adult survival might be improved by increasing the quantity or quality of available host plants, the citrus plant used in this study was a suitable host to support long-term survival (>8 mo at 23.4°C) without showing any stress symptoms at temperatures tested herein. Although cowpea plant is a suitable feeding host for *H. vitripennis* (Setamou and Jones 2005), it did not tolerate stress when exposed to low and high temperatures in our preliminary test and was found to be inappropriate for the constant-temperature experiment because of its narrow temperature range of physiological tolerance.

Under field conditions, *H. vitripennis* adults have a variety of feeding hosts available (Hoddle et al. 2003), and they can seek better host plant species and/or plant developmental stages through long-distance flight (Blackmer et al. 2004). Such an ability would provide an adaptive advantage to escape hostile temperature conditions and to seek microhabitats that are more favorable. Consistent with our laboratory observations, Pollard and Kaloostian (1961) reported that *H. vitripennis* adults dropped off the plant on exposure to low winter temperatures in the field. Such adult behavioral responses could increase their survival when cold stressed, because the soil temperature is often higher than ambient air temperature at nights in winter (Rosenberg 1974), and leaf litter on the soil surface in the field can provide additional protection from the cold stress (Shields and Sher 1992, Lam and Pedigo 2000).

In southern California, where *H. vitripennis* has been well established, densities of reproductive adults decline sharply over winter, but in the following generation (June–July) reach the highest densities of the year (Blua et al. 2001, Castle et al. 2005). The survival of overwintering adults is crucial to *H. vitripennis* population growth in the springtime to guarantee permanent populations in newly colonized locations. New information herein has implications for the temperature conditions required for mass rearing and bioassays, as well as for delimiting the potential range of this invasive species as an influential vector of PD.

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