Influence of Light on Reproductive Rates of Asian Citrus Psyllid (Hemiptera: Liviidae)

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Abstract

The impact of light on reproductive rates of Asian citrus psyllid (Diaphorina citri Kuwayama) was assessed in an air-conditioned, polycarbonate greenhouse. This psyllid is an important pest because it transmits a bacterium presumed responsible for a serious citrus disease known as Asiatic huanglongbing. Numbers of psyllids produced were compared among rearing cages subjected to different amounts of light provided by natural sunlight and light-emitting diode floodlights. Light to some rearing cages was purposely reduced by shading. The cages received a daily mean of 12 h of light (range 7 to 14 h) during immature development. Irradiance during daylight hours in the cages during a 24-h oviposition period varied from 2 to 145 (mean 66) W/m² and during immature development to the adult stage from 3 to 169 (mean 71) W/m². Estimates of illuminance during immature development ranged from 354 to 73,500 (mean 22,409) lumens/m². Oviposition rates were not correlated with these light variables. Numbers of adults produced were positively correlated with daily hours of light (r = 0.57, P = 0.002), irradiance (r = 0.39, P = 0.05), and illuminance (r = 0.59, P = 0.001). For producing large numbers of adults, optimal targets for these light variables as measured in this study were projected to be 14 or more hours of daylight, 60 or more W/m², and 20,000 or more lumens/m². Comparisons of oviposition rates and resulting numbers of adults produced in a cage indicated that increasing these light variables increased survival of immatures to the adult stage, possibly because the quality of host plants increased as these light variables increased.

Key words: Diaphorina citri, citrus greening, huanglongbing, irradiance, illuminance

The Asian citrus psyllid, Diaphorina citri Kuwayama, is an important invasive pest of citrus in North America because it vectors ‘Candidatus Liberibacter asiaticus’ Jagoueix et al. (Rhizobiaceae: Rhizobiales: Rhizobiaceae), a bacterium presumed to be responsible for a serious citrus disease known as Asiatic huanglongbing (also known as citrus greening or yellow shoot disease; Halbert and Manjunath 2004, Bové 2006). Management tactics aimed at preventing the introduction and spread of the disease in citrus orchards have largely been ineffective and once trees are infected, there is no cure for the disease. The Asian citrus psyllid is thought to be southwest Asia in origin and the disease was first described in Asia, but both the vector and bacterium have invaded many citrus-growing areas around the world. Following the 1998 discovery of the psyllid in the United States (Florida) and the subsequent 2005 discovery of huanglongbing, the sweet orange and grapefruit industries in Florida have seriously been jeopardized (Hodges and Spreen 2012, Alvarez et al. 2016). Researchers and growers continue struggling to find solutions.

Many research endeavors seeking solutions to huanglongbing are dependent on colonies of Asian citrus psyllid reared in laboratory or greenhouse settings. The USDA in Fort Pierce, Florida many years ago established insectary colonies of the psyllid in an air-conditioned, polycarbonate (GE 8mm Twin Wall, Lexan Thermoclear, San Diego Plastics, Inc., National City, CA) greenhouse. Cages of Asian citrus psyllid on potted host plants are maintained on wire shelving under natural sunlight. Initially there was a single shelf of cages around the greenhouse, but later a second shelf was added below the first shelf. Eventually thousands of psyllids were needed weekly; thus, rearing was expanded to a three-shelf arrangement accommodating dozens of rearing cages. General observations revealed that numbers of psyllids produced per cage were largest on the top shelf and lowest on the bottom shelf. This was perceived primarily as a lighting issue, a consequence of differences in irradiance (solar radiation) or illuminance (light intensity) or both. The initial remedy was to allow oviposition and early development of nymphs to take place in cages on the top shelf, moving cages to the middle and ultimately the lowest shelf as nymphs progressed through the third to fifth instars. Later, cages on the middle and bottom shelves were provided supplemental lighting (light-emitting diode [LED] floodlights outside of a cage aimed at the plants inside). Cages on the top shelf were not provided supplemental lighting. The changes in lighting increased psyllid...
production on the lower shelves. Eventually the questions arose as to how much supplemental lighting was needed and whether supplemental lighting would enhance production on the upper shelf, particularly during cloudy periods of time and under shorter photoperiods in winter.

The primary objectives of research presented here were to assess the influence of irradiance and illuminance on Asian citrus psyllid production parameters, specifically 1) oviposition rates, 2) numbers of adults produced, and 3) developmental rates from oviposition to emergence of new adults. In addition, of interest were biological parameters associated with adult psyllids produced under different light regimes including sex ratios, abdominal color of newly emerged adults, and the occurrence of adults with wing deformities, the latter of which are sometimes observed (Hall and Hentz 2016).

Methods and Materials

The influence of irradiance and illuminance on reproductive rates of Asian citrus psyllids in rearing cages was assessed by subjecting different rearing cages to different amounts of light. The experiment was repeated 5 times in the following order, with natural light and different amounts of supplemental lighting each time: late fall, winter, spring, mid-summer, and late summer.

Research Setting

Adults of the Asian citrus psyllid for these studies were obtained from the aforementioned USDA insectary colony, established in 2000 using psyllids field-collected from citrus and subsequently reared in cages (BugDorm-2, BD2120F; MegaView Science Education Services Co., Ltd., Taichung, Taiwan) in the air-conditioned greenhouse (roof and upper walls made of the polycarbonate panels described above). Details of the colony have previously been reviewed (Hall et al. 2015). Citrus macrophylla Wester has been used as the rearing plant since 2010. The insectary colony is maintained using procedures similar to those described by Skelley and Hoy (2004), with no infusion of wild types. The insectary colony is subdivided among many cages (up to 78 at a time) containing psyllids at various different stages of growth and age.

The greenhouse air conditioner maintains an average annual air temperature of about 25°C, measured in the center of the greenhouse 2.5 m above the floor. However, during winter and summer, the temperature has averaged around 22 and 27°C, respectively. The greenhouse is fitted with an automatic ceiling shade cloth programed to provide shade from the hours of 1300 to 1700 each day (civil time during two winter repetitions and daylight savings time for the other three repetitions). The shade cloth is important for reducing excessively high temperatures during the afternoon. With shade in place, maximum daily temperatures at the center of the greenhouse during summer afternoons are usually maintained below 32°C, but temperatures before 1300 h are sometimes higher.

Rearing Procedures and Production Data

Except where noted, the research presented here followed the same rearing procedures routinely used to maintain the USDA insectary colony. Citrus macrophylla plants for insectary cages are grown in 3.8-liter pots (model C300S, Universal Enterprises Supply Corp., Pompano Beach, FL) containing steamed (sterilized) Pro-Mix BX (Premier Horticulture, Inc., Quakertown, PA) and are trimmed to stimulate a flush of new leaf growth when the plants are 20 to 25 cm tall. Stems of new leaf growth are commonly referred to as flush shoots (Hall and Albrigo 2007) and are essential for oviposition and nymph development. When new flush begins to emerge, a new insectary colony cage is established using four plants per cage (two on the north and two on the south side of a cage), each plant usually with 10 to 15 new flush shoots. For the study presented here, each plant was standardized to have 11 or 12 new flush shoots per plant. Approximately 300 adult psyllids (10 to 14 d old, no attention to sex) are introduced and allowed to oviposit for 3 d. For the study presented here, 300 adults were allowed to oviposit for 24 h. The adults are then removed from the plants by shaking each plant vigorously in the cage to dislodge the adults, removing the plants from the cage and aspirating from each plant any remaining adults. The four plants with fresh eggs are transferred to a clean cage, which is then placed onto a rearing shelf. Eggs are allowed to hatch and nymphs develop to the adult stage. The potted plants are maintained in drip pans, to which tap water is added twice a week. A general purpose 20N-10P-20K water-soluble fertilizer mix (Peters Professional, The Scotts Company, Marysville, OH) is applied once a week when watering.

Oviposition dates for the five repetitions of the experiment: for late fall, 15–16 November; for winter, 17–18 January; for spring, 12–13 April; for mid-summer, 16–17 July; and for late summer, 31 August–1 September. After 24 h of oviposition, four typical flush shoots (one from each cardinal section of each plant) were removed from each plant and examined under a dissecting microscope to count the number of eggs per shoot. The specific plant from which shoots were taken was recorded in all but the first repetition. For the first four repetitions, the cages were monitored until new adults first began emerging, at which point new adults were removed from cages daily, which allowed calculation of initial and peak emergence periods. We ceased monitoring a set of cages for new adults when none was found in some cages, few were found in other cages, and there appeared to be an absence of mature nymphs remaining on the plants. Data collected included the number of adults emerging each day, their sex, the color of their abdomen (gray/brown, blue/green, or yellow/orange as described by Wenninger et al. 2009), and the number with wing deformities. For the late summer repetition, the cages were monitored during weekdays, new adults were removed daily on weekdays until emergence was over, and the total number of adults produced was determined. Since the cages were not observed on weekends, we were unsure when emergence began in two of the cages of this repetition, and peak emergence could not be identified in any of the cages. No data were collected on color morphs or wing deformities during the late summer repetition. For all repetitions of the experiment, the total number of adults collected from a cage was divided by the number of flush shoots in the cage (excluding the four removed for egg counts) to estimate the number of adults produced per flush shoot. An index of immature survival to the adult stage was taken as the mean number of adults produced per shoot in a cage divided by the mean number of eggs per flush shoot in the cage—an index value of 1.0 indicated that all eggs made it to the adult stage, with decreasing values indicating increasingly poorer survival.

Experimental Setup and Supplemental Lighting

Six rearing cages were utilized for the experiment, two on each of an upper, middle, and lower shelf (Supp Fig. 1 online only]). The shelves were located along a wall in the northeast corner of the greenhouse (total floor area 9.6 m²), with cage entranceways facing south. The walls behind and to the east of cages on the lower shelf were concrete block while the walls behind and to the east of cages on the upper two shelves were made of polycarbonate panels. Each time the experiment was conducted, some cages received
supplemental lighting, and some did not. For cages subjected to supplemental lighting, 14 h of daily light were provided from the hours of 0600 to 2000, with no artificial lighting anywhere within the greenhouse after 2000 h each day. The cages received supplemental lighting provided by LED floodlights (EnduralLED Par 38, 22 degree, Phillips Lighting, Somerset, NJ) in a fixture (21.5 cm aluminum reflector, Utility Clamp Work Light, Globe Electric; Montreal, Quebec Canada) clamped to a wooden stand beside a cage or to the shelf above a cage. The lights were rated at 930 lumens output, 17 W, color rendering index of 85, and 3,000 K color temperature. The six cages were maintained in the same position during all five repetitions of the experiment, but the amount of supplemental lighting to a cage varied using from 0 up to 6 flood lights per cage with lights positioned 6 to 15 cm from the upper side of a cage, for a 6.25 range of light intensities (152/62). In both the mid-summer and late summer repetitions, a cage on the bottom shelf received no supplemental lighting and was shaded using cardboard on all sides except the entrance side (Supp Fig. 1B [online only]). In the late-summer repetition, a cage on the bottom shelf received no supplemental lighting, was shaded on five sides with cardboard, and the entrance side was loosely covered with a black cloth (low levels of light penetrated the cage; Supp Fig. 1C [online only]).

Irradiance expressed as W/m² was monitored in the center of each cage approximately 34 cm above the floor of the cage (at or just above the upper canopy level of the four plants, see Supp Fig. 1E–G [online only]) using a WatchDog silicon pyranometer sensor (#36701, 3670/WS2, Spectrum Technologies, Inc., Aurora, IL). The pyranometer sensor measured solar radiation between 300 and 1100 nm and was connected to a Watchdog 1450 Micro Station (#3684WD1, Spectrum Technologies, Inc.), which simultaneously monitored air temperature and humidity. The Micro Station was positioned in a radiation shield at the center of each cage about 18 cm above the floor of the cage. The silicon pyranometer and Micro Station were attached to a metal stand (Supp Fig. 1D [online only]).

Ultraviolet radiation was monitored throughout the study in one cage on the top shelf using a Watchdog UV light sensor (#36761, Spectrum Technologies, Inc.) connected to the cage’s Micro Station. This sensor, which monitored radiation between 230 and 400 nm, was attached to the metal stand such that it was close to and at the same height above the cage floor as the silicon pyranometer sensor. This cage received supplemental lighting during three of the experiments (Supp Table 1 [online only], cage #2).

Solar radiation, temperature, humidity, and ultraviolet light were recorded every 15 min from when adult psyllids were introduced into cages for oviposition to when emergence of progeny adults was considered complete. These data were then downloaded to a computer using SpecWare 9 Professional (Spectrum Technologies, Inc.). An average W/m² based on the four measurements per hour was calculated, and J/m²/s (1 W = 1 J/s) was converted to Megajoules (MJ) per hour (MJ/m²/h): (J/m²/s) * 3,600/1,000,000. Megajoules/m²/day (MJ/m²/d) was then calculated by summing MJ/m²/h values each day.

Illuminance (expressed as lux = lumens/m²) was monitored at approximately the same location in each cage that solar radiation was monitored. A Dual-Range Light Meter (Model 06-662-63 with a Traceable Certificate of Calibration #3251-8702572; Control Company, Webster, TX) was used to measure illuminance. The meter was manufactured for and distributed by Fisher Scientific, Pittsburgh, PA. Illuminance was measured on sunny days within 1 h before the shade cloth opened (no shade) and within 1 h after the shade cloth opened (shade provided).

### Statistical Analyses

A paired t-test (PROC TTEST, SAS Institute 2012) was used to compare numbers of eggs laid on the north and south plants in each rearing cage across repetitions 2–5. Correlation analyses (Pearson’s coefficient) were conducted to investigate the statistical relationships between each environmental variable and numbers of Asian citrus psyllid produced per shoot (eggs laid per shoot and adults produced per shoot), developmental rates of immatures, and indices of immature survival using PROC CORR (SAS Institute 2012). The relationships were similarly investigated between the environmental variables and adult sex ratios, percentages of new adults of each color morph, and percentages of adults with wing deformities. Data on numbers of eggs laid per shoot, adults produced per shoot, and indices of immature survival were subjected to simple linear regressions using PROC GLM (SAS Institute 2012).

### Results and Discussion

The environmental factors studied were measured at the center of a cage. The measurements therefore represent relative values for a cage and not the specific amounts of irradiance and illuminance associated with individual plants. The amount of light reaching plants in cages with supplemental lighting was probably higher than the relative amount measured in the center of a cage.

Low levels of persistent irradiation at night were detected in one cage during the first experimental repetition but only during oviposition; thus, data on irradiance in this cage were excluded from correlation analyses on oviposition. In addition, low levels of persistent irradiation at night were detected in a second cage during the first,

### Table 1. Simple statistics for oviposition rates and environmental factors during oviposition

| Variable              | N<sup>a</sup> | Mean | Standard deviation | Minimum | Maximum |
|-----------------------|---------------|------|--------------------|---------|---------|
| Number of eggs/shoot  | 30            | 39.9 | 16.9               | 15.4    | 78.1    |
| Temperature (°C)      | 30            | 26.4 | 2.0                | 23.1    | 29.6    |
| Percent humidity      | 30            | 57.4 | 10.2               | 37.6    | 71.1    |
| Irradiance, W/m²      | 26            | 66.4 | 42.6               | 1.6     | 144.6   |
| Maximum W/m²          | 26            | 183.9| 124.4              | 3.0     | 436.0   |
| Total hours of light  | 26            | 12.4 | 3.4                | 2.3     | 16.0    |
| Cumulative MJ/m²      | 26            | 3.5  | 2.5                | 0.02    | 8.7     |
| Lux, lumens/m²        | 30            | 21,662| 20,073            | 11      | 73,500  |
| Minimum lumens/m²     | 30            | 16,151| 18,001            | 3       | 57,000  |
| Maximum lumens/m²     | 30            | 27,552| 23,615            | 23      | 90,000  |

<sup>a</sup>N refers to the number of data values (one from each rearing cage) per variable and is the number of data values used for each correlation analysis in Table 2.
second, and third repetitions during oviposition and the development of immatures; thus, data on irradiance in this cage were excluded from all correlation analyses. The silicon pyranometer sensor in this cage was replaced with a new unit for the fourth and fifth repetitions.

The average oviposition rate was 40 eggs/flush shoot/24 h and ranged from 15 to 78 (Table 1). Depending on repetition and location of rearing cages, air temperature during oviposition averaged from 23.1 to 29.6°C and relative humidity averaged from 38 to 71% (Table 1; Supp Table 1 [online only]). Total cumulative hours of light during oviposition over the 24-h period ranged from 2.3 to 16.0 h. Irradiance during oviposition averaged from 2 to 145 W/m² with maximums of 3 to 436 W/m², and cumulative irradiance averaged from 0.02 to 8.7 MJ/m². Illuminance during oviposition averaged from 11 to 73,500 lumens/m² at the center of the cages. No ultraviolet light was detected, supporting reports that the polycarbonate material of the greenhouse roof is opaque to radiation in the UV region and confirming that the LED lights did not contribute ultraviolet light. Within the range of these conditions, none of the environmental variables was correlated with rates of oviposition (Table 2). At levels above and below those in this study, temperature and humidity are known to influence oviposition rates (Tsai and Liu 2000, Skelley and Hoy 2004, Hall et al. 2011, Alves et al. 2014). Oviposition rates during each repetition of the experiment were similar among the six cages, including the fourth and fifth repetitions when one or two cages were purposely shaded (Supp Table 1 [online only]). Although average oviposition rates in a cage were not correlated with light (Table 2; Fig. 1), numerically greater numbers of eggs were laid on plants on the south sides of cages. Means ± SEM of 57.1 ± 5.1 and 18.4 ± 2.0 eggs per flush shoot were laid on south and north plants, respectively—these means were significantly different ($t = -6.2, P \leq 0.0001, DF 23$). This difference was attributed to attraction of adults to light, of which visually there was more of on the south side of the cages.

Environmental conditions during development of immatures varied among the experimental repetitions depending on time of year, location of rearing cages, and supplemental lighting (Table 3; Supp Table 2 [online only]). Since no ultraviolet light was detected, measurements of irradiance were accurate for wavelengths from 400 up to 1100 nm.

New adults began emerging from 13 to 18 d after oviposition, peak emergence occurred 15 to 21 d after oviposition, and the median days from oviposition to emergence ranged from 19 to 24 d (Table 3; Supp Table 3 [online only]). Developmental time (median days to emergence and peak days to emergence) was negatively correlated with mean and minimum daily air temperature (Table 4). Developmental rates of immatures are known to be influenced by temperature (Liu and Tsai 2000, Nava et al. 2007, Alves et al. 2014). Depending on the repetition, emergence of new adults was completed within 8 to 14 d after the first new adults emerged. The number of adult Asian citrus psyllids produced in the cages ranged from 3.8 to 64.4 adults/flush shoot (Table 3). Numbers of adults produced were positively correlated with oviposition rates, irradiation, illuminance, and daily hours of light (Fig. 2) and not correlated with air temperature or humidity (Table 4). Although we only investigated the simple linear relationship between numbers of adults produced and the light variables, other relationships could be investigated using the data in Supp Tables 2 and 3 (online only). Since light positively influenced numbers of adults produced in a cage but had no effect on oviposition rate, reductions in numbers of adults produced under low lighting can be attributed to reduced survival of eggs or nymphs. This was reflected in survival indices, which were positively correlated with light (Table 4; Fig. 2). Noted is that survival indices associated with five cages exceeded 1.0, which was attributed to sampling error in estimating egg densities. These five index values were not excluded from correlation and regression analyses. Poorer survival of immatures under low light conditions may have been related to changes in their host plants, possibly reduced rates of photosynthesis, or translocation of water and nutrients. During the fifth repetition of the experiment in the heavily shaded cage, most flush shoots

Table 2. Results of correlation analyses on numbers of eggs per flush shoot and environmental conditions during oviposition

| Independent variable | Number eggs per shoot | $r$ | $P$ |
|----------------------|-----------------------|-----|-----|
| Temperature (°C)     | 0.30                   | 0.11|     |
| Relative percent humidity | 0.24 | 0.20|     |
| Irradiance, W/m²     | 0.05                   | 0.83|     |
| Maximum W/m²         | -0.10                  | 0.64|     |
| Total hours of light | 0.22                   | 0.28|     |
| Cumulative MJ/m²     | 0.01                   | 0.94|     |
| Lux, lumens/m²       | 0.22                   | 0.24|     |
| Minimum lumens/m²    | 0.21                   | 0.26|     |
| Maximum lumens/m²    | 0.22                   | 0.25|     |

Fig. 1. Numbers of eggs laid by Asian citrus psyllid over a 24-h period were not influenced by total number hours of light nor by levels of irradiance (W/m²) during these light hours.
aborted within several days after oviposition—although some immatures in this cage made it to the adult stage, data on adult numbers produced in this cage were excluded from the correlation analyses.

Sex ratios were not correlated with any of the environmental parameters (Supp Tables 4 and 5 [online only]). Few newly emerged adults were of the yellow/orange morph, which agreed with observations on newly emerged adults by Wenninger and Hall (2008). No significant correlations were found between adult color and light. Maximum air temperature was negatively correlated with percentages of adults of the gray/brown morph and positively correlated with percentages of adults of the blue/green morph, but reasons these differences might exist were not known. Hemocyanin may in part be responsible for the blue/green color (Ramsey et al. 2017), but why some psyllids might contain more hemocyanin than others might or if higher temperatures promote hemocyanin production is not known. Based on correlation analyses, reduced light (lumens/m²

### Table 3. Simple statistics for the correlation analyses on oviposition rates, numbers of adult Asian citrus psyllid produced, and average daily environmental factors

| Variable                        | N* | Mean | Standard deviation | Minimum | Maximum |
|---------------------------------|----|------|--------------------|---------|---------|
| Number eggs/shoot               | 29 | 45.0 | 16.4               | 17.9    | 78.0    |
| Days to peak adult emergence    | 24 | 17.7 | 2.0                | 15.0    | 21.0    |
| Median days to emergence        | 28 | 21.3 | 1.7                | 19.0    | 24.0    |
| Number adults/shoot             | 29 | 31.5 | 19.2               | 3.8     | 64.4    |
| Survival index                  | 29 | 0.7  | 0.4                | 0.1     | 1.8     |
| Temperature (°C)                | 29 | 26.1 | 1.5                | 23.9    | 28.5    |
| Minimum temperature             | 29 | 23.0 | 2.5                | 20.3    | 26.2    |
| Maximum temperature             | 29 | 32.2 | 2.9                | 27.4    | 40.9    |
| Percent humidity                | 29 | 61.7 | 3.9                | 54.5    | 70.6    |
| Hours of daily light             | 26 | 12.3 | 2.1                | 6.5     | 14.1    |
| Irradiance, W/m²                | 26 | 71.3 | 44.6               | 3.2     | 168.8   |
| Maximum W/m²                    | 26 | 189.7| 112.2              | 10.2    | 414.9   |
| MJ/m²/d                         | 26 | 3.6  | 2.5                | 0.1     | 9.0     |
| Lux, lumens/m²                  | 29 | 22,409| 20,000            | 354     | 73,500  |
| Minimum lumens/m²               | 29 | 16,708| 18,055            | 151     | 57,000  |
| Maximum lumens/m²               | 29 | 28,501| 23,444            | 847     | 90,000  |

*N refers to the number of data values (one from each rearing cage) per variable and is the number of data values used for each correlation analysis in Table 4.

### Table 4. Results of correlation analyses on numbers of adults produced per flush shoot. An asterisk next to an r correlation coefficient indicates significance.

| Variable                        | Number of adults | Immature survival index | Median days to emergence | Days to peak adults |
|---------------------------------|------------------|-------------------------|--------------------------|---------------------|
| Number of adults                | r 1.0            | 0.83*                   | 0.12                     | −0.39               |
|                                 | P <0.0001        | 0.55                    | 0.06                     |
| Number eggs                     | r 0.41*          | −0.08                   | −0.32                    | −0.52*              |
|                                 | P 0.03            | 0.67                    | 0.10                     | 0.01                |
| Temperature                     | r 0.21           | 0.01                    | −0.89*                   | −0.89*              |
|                                 | P 0.26            | 0.96                    | <0.0001                  | <0.0001             |
| Minimum temperature             | r 0.02           | −0.23                   | −0.92*                   | −0.86*              |
|                                 | P 0.93            | 0.24                    | <0.0001                  | <0.0001             |
| Maximum temperature             | r 0.08           | 0.22                    | 0.00                     | 0.12                |
|                                 | P 0.67            | 0.25                    | 0.99                     | 0.56                |
| Humidity                        | r −0.19          | −0.42*                  | −0.70*                   | −0.51*              |
|                                 | P 0.33            | 0.02                    | <0.0001                  | 0.01                |
| Irradiance, W/m²                | r 0.39*          | 0.61*                   | 0.15                     | −0.14               |
|                                 | P 0.05            | 0.001                   | 0.47                     | 0.53                |
| Maximum W/m²                    | r 0.36           | 0.55*                   | 0.44*                    | 0.17                |
|                                 | P 0.07            | 0.004                   | 0.03                     | 0.45                |
| Daily light hours               | r 0.37           | 0.59*                   | 0.08                     | −0.21               |
|                                 | P 0.06            | 0.002                   | 0.70                     | 0.35                |
| MJ/m²/d                         | r 0.57*          | 0.61*                   | −0.03                    | −0.44*              |
|                                 | P 0.002           | 0.001                   | 0.89                     | 0.05                |
| Lux, lumens/m²                  | r 0.59*          | 0.68*                   | 0.27                     | −0.05               |
|                                 | P 0.001           | <0.0001                 | 0.16                     | 0.81                |
| Minimum lumens/m²               | r 0.53*          | 0.60*                   | 0.13                     | −0.13               |
|                                 | P 0.003           | 0.001                   | 0.52                     | 0.55                |
| Maximum lumens/m²               | r 0.61*          | 0.69*                   | 0.35                     | −0.00               |
|                                 | P 0.0004         | <0.0001                 | 0.07                     | 0.98                |
and W/m²) may have been associated with increases in percentages of adults with wing deformities (Supp Table 5 [online only]).

Changes in sunlight have previously been shown to affect different aspects of the biology and behavior of Asian citrus psyllid. For example, adult flight activity is strongly influenced by sunlight (Aubert and Xia 1990). Working with adult psyllids placed under different light regimes (from 1,200 to 15,000 lumens/m² and from 6 to 18 h of daily illumination), Yang (1989) reported that newly emerged females began laying eggs sooner (shorter preoviposition period), lived longer, and laid more eggs over their life as light intensity and photoperiod increased. Our research differed from Yang’s in that we studied oviposition rates over a 24-h period by females already mating and laying eggs. Results of research presented here indicated that survival rates of immatures to the adult stage vary depending on irradiance, illuminance, and day length. Anecdotal evidence exists that citrus is colonized by fewer Asian citrus psyllids under low light situations and that severity of huanglongbing is reduced. The evidence includes observations of citrus grown in pots under the canopies of large oak trees near commercial citrus (Hall, personal observations) and in citrus planted in the shade of banana plants (observations by B. Bowman, University of Florida). Citrus planted in the shade of guava trees in Vietnam was infested by fewer psyllids and was less affected by huanglongbing than citrus not planted under guava (Hall, personal observations; Gottwald et al. 2014). Lower infestation levels of the psyllid on citrus under shade could be a result of adults being less likely to find shaded citrus or being more attracted to citrus in full sun. If adults find and colonize citrus under shade, oviposition rates would be reduced if shade promotes cooler air temperatures (Hall et al. 2011). Based on the current study, if oviposition occurs on citrus under shade, fewer immatures would develop to the adult stage depending on the amount of shade. Of interest is if shading could be an applied component of an IPM program against the Asian citrus psyllid and huanglongbing. Monzo and Stansly (2017) reported that yield losses to huanglongbing were lowest in citrus harboring the fewest psyllids, and infestation thresholds for the decision to apply insecticides for psyllid control were obtained—for citrus under shade, these thresholds could be reference points as to how much shade might be needed at least in mature trees.

In summary, oviposition rates per 24 h by Asian citrus psyllid were not affected by photoperiod, irradiance, or illumination under the conditions of this study. After oviposition, supplemental light may be required in an insectary to ensure that large percentages of immatures successfully develop to the adult stage. Longer photoperiods should be beneficial—a 14-h photoperiod was the maximum studied here, but a longer photoperiod may be optimal (Yang 1989). Based on the rearing procedures presented here, illumination above 20,000 lumens/m² and irradiance above 60 W/m² at the center of a cage should generally promote better survival of immatures and thus produce greater numbers of adults. For the USDA insectary, the results of the research support supplemental lighting for all rearing cages.

**Supplementary Data**

Supplementary data are available at Journal of Insect Science online.

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for introducing us to the Inverse Square Law formula. Mention of a trademark or proprietary product is solely for the purpose of providing specific information and does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products that may also be suitable. USDA is an equal opportunity provider and employer.

References Cited

Alvarez, S., E. Rohrig, D. Solis, and M. H. Thomas. 2016. Citrus greening disease (huanglongbing) in Florida: economic impact, management and the potential for biological control. Agric. Res. 5: 109–118.

Alves, G. R., A. J. Diniz, and J. R. Parra. 2014. Biology of the Huanglongbing vector Diaphorina citri (Hemiptera: Liviidae) on different host plants. J. Econ. Entomol. 107: 691–696.

Aubert, B., and Y. H. Xia. 1990. Monitoring flight activity of Diaphorina citri on citrus and Murraya canopies, pp. 181–187. In B. Aubert, S. Tontyaporn, and D. Buangsuwon (eds.), Rehabilitation of citrus industry in the Asia pacific region. FAO-UNDP, Rome, Italy.

Bové, J. M. 2006. Huanglongbing: a destructive, newly-emerging, century-old disease of citrus. J. Plant Pathol. 88: 7–37.

Gottwald, T. R., D. G. Hall, A. B. Kris, E. J. Salinas, P. E. Parker, G. A. C. Beattie, and M. C. Nguyen. 2014. Orchard and nursery dynamics of the effect of interplanting citrus with guava for huanglongbing, vector and disease management. Crop Prot. 64: 93–103.

Halbert, S. E., and K. L. Manjunath. 2004. Asian citrus psyllids (Sternorrhyncha: Psyllidae) and greening disease of citrus: a literature review and assessment of risk in Florida. Fla. Entomol. 87: 330–353.

Hall, D. G., and L. G. Albrigo. 2007. Estimating the relative abundance of flush shoots in citrus, with implications on monitoring insects associated with flush. HortScience 42: 364–368.

Hall, D. G., and M. G. Hentz. 2016. An evaluation of plant genotypes for rearing Asian citrus psyllid (Hemiptera: Liviidae). Fla. Entomol. 99: 471–480.

Hall, D. G., E. J. Wenninger, and M. G. Hentz. 2011. Temperature studies with the Asian citrus psyllid, Diaphorina citri Kuwayama: cold hardness and temperature thresholds for oviposition. J. Insect Sci. 11: 1–15.

Hall, D. G., M. G. Hentz, and J. M. Patt. 2015. Behavioral assay on Asian citrus psyllid attraction to orange jasmine. J. Insect Behavior. 28: 553–568.

Hodges, A. W., and T. H. Spreen, 2012. Economic impacts of citrus greening (HLB) in Florida, 2006/07–2010/11. University of Florida, Institute of Food and Agricultural Sciences, Gainesville. EDIS document FE903, Food and Resource Economics Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville. pp. 6.

Huanglongbing (HLB) in Florida, 2006/07–2010/11. University of Florida, Institute of Food and Agricultural Sciences, Gainesville. EDIS document FE903, Food and Resource Economics Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville. pp. 6.

Liu, Y. H., and J. H. Tsai. 2000. Effects of temperature on biology and life table parameters of the Asian citrus psyllid, Diaphorina citri Kuwayama (Homoptera: Psyllidae), Annals Appl. Biol. 137: 201–206.

Monzo, C., and P. A. Stansly. 2017. Economic injury levels for Asian citrus psyllid control in process oranges from mature trees with high incidence of huanglongbing. PLoS One 12: e017533.

Nava, D. E., M. L. G. Torres, M. D. L. Rodrigues, J. M. S. Bento, and J. R. P. Parra. 2007. Biology of Diaphorina citri (Hem., Psyllidae) on different hosts and at different temperatures. J. Appl. Entomol. 131: 709–715.

Ramsey, J. S., J. D. Chavez, R. Johnson, S. Hosseinzadeh, J. Mahoney, J. Mohr, F. Robison, X. Zhong, D. G. Hall, M. MacCoss, et al. 2017. Protein interaction networks at the host-microbe interface in Diaphorina citri, the insect vector of the citrus greening pathogen. R. Soc. Open Sci. 4: 160545.

SAS Institute, Inc. 2012. SAS procedures guide. Version 9.4. SAS Institute, Cary, NC.

Skelley, L. H., and M. A. Hoy. 2004. A synchronous rearing method for the Asian citrus psyllid and its parasitoids in quarantine. Biol. Control 29: 14–23.

Wenninger, E. J., and D. G. Hall. 2008. Daily and seasonal dynamics in abdominal color in Diaphorina citri (Hemiptera: Psyllidae). Annals Entomol. Soc. America. 101: 585–592.

Wenninger, E. J., L. L. Stelinski, and D. G. Hall. 2009. Relationships between adult abdominal color and reproductive potential in Diaphorina citri (Hemiptera: Psyllidae). Annals Entomol. Soc. America. 102: 476–483.

Yang, Y. B. 1989. Effects of light, temperature and humidity on the development, reproduction and survival of citrus psylla. Acta Ecol. Sin. 9: 348–354.