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Source: Florida Entomologist, 89(3) : 340-347

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/0015-4040(2006)89[340:EOTALO]2.0.CO;2

EFFECT OF TEMPERATURE AND LENGTH OF EXPOSURE TIME ON PERCENT EGG HATCH OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

The oligophagous cactus moth, *Cactoblastis cactorum* (Berg), has been recognized as a serious and immediate threat to *Opuntia* cacti in Florida and the southeastern United States. The moth has successfully colonized new geographical ranges with lower annual temperatures north of the Florida Keys where it was first detected in the continental United States in 1989. This study evaluated the effect of temperature on egg development and egg hatch of *C. cactorum* by utilizing various treatment temperatures, exposure times, and egg ages. The temperatures used in this study ranged from a low of -20°C to a high of 50°C, thus encompassing the potential range of temperatures that eggsticks may be exposed to in potential new host areas. One-d-old eggs held at a constant temperature of 30°C resulted in the highest percent hatch and shortest time to egg hatch. Eggs did not hatch when held at constant temperatures ≤15°C or ≥35°C. Furthermore, one d of exposure at -10°C and 4 d of exposure at -5°C were 100% lethal to one-d-old eggs. Eggs that were 7- and 14-d-old before exposure to cold temperatures were generally more resistant to temperature effects than one-d-old eggs.

Key Words: cactus moth, invasive species, insect development

RESUMEN

La polífaga palomilla del cactus, *Cactoblastis cactorum* (Berg), ha sido reconocida como una amenaza seria e inmediata a las cactáceas del género *Opuntia* presentes en el estado de Florida y en el sureste de los Estados Unidos de América. La palomilla ha sido exitosa en la colonización de nuevas áreas geográficas que poseen temperaturas mas bajas que el area en los Cayos de Florida donde la plaga fue detectada por primera vez en 1989. En este estudio se evaluaron los efectos de temperatura sobre el desarrollo de huevecillos y la eclosión de neonatos de la palomilla del cactus. Los huevecillos fueron expuestos a varias temperaturas por periodos de tiempo diferentes y se realizaron experimento con huevecillos de distintas edades. Las temperaturas utilizadas en este estudio variaron desde una temperatura baja de -20°C a una temperatura alta de 50°C, rangos que abarcan las temperaturas a las que los huevecillos podrian estar expuestos si la palomilla coloniza nuevas areas. Los huevecillos de un dia de edad que se mantuvieron a una temperatura constante de 30°C mostraron el porcentaje de eclosion mas alto y el tiempo de eclosion mas corto. Los huevecillos no tuvieron emergencia de neonatos cuando fueron expuestos a temperaturas de 35°C o 15°C. Asimismo, no se obtuvo emergencia de neonatos cuando los huevecillos fueron expuestos a una temperatura de -10°C por un dia o a una temperatura de -5°C por 4 dias. Los huevecillos de siete y catorce dias de edad que fueron expuestos a temperaturas bajas se mostraron mas resistentes que los huevecillos de un dia de edad.

Translation by authors

The cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), was first recorded in North America in the Florida Keys in 1989 (Habeck & Bennett 1990; Stiling & Moon 2001). This insect feeds on prickly pear cactus (*Opuntia* spp.) and is native to South America, but has been transported around the world to control exotic pestiferous *Opuntia* spp. in Australia, South Africa, Hawaii, and numerous other countries (Zimmermann et al. 2000). The moth was introduced to Nevis in the Caribbean in 1957 to control native *Opuntia* spp. that were becoming weedy on

disturbed pasture land (Simmons & Bennett 1966). Heppner (2000) documents the spread of *C. cactorum* through the Caribbean Islands aided by deliberate introductions and natural dispersion.

Adult cactus moths mate in the early morning (Hight et al. 2003) and oviposition on cactus usually begins the following evening. Eggs are laid on top of one another forming eggsticks that are normally attached to cactus spines or directly to cactus pads. Larvae emerge synchronously and together penetrate the thick outer layer of the host plant, then move to feed inside cactus pads (Robertson 1989). After a pad has been completely consumed, larvae tunnel to other pads through the nodes or leave the destroyed pad to seek other undamaged host material. Larvae may inhabit all portions of the cactus plant, including roots, and, with the aid of associated rot organisms, the entire cactus plant may be killed (Sweetman 1958). Dodd (1940) and Pettey (1948) documented the effect of field temperatures on the phenology, fecundity, and life cycle of *C. cactorum* in Australia and South Africa, respectively. Dodd (1940) reported that eggsticks and pupae have high mortality when exposed to "unseasonably" high or low temperatures. Larvae faired better because they were able to move within the plant and thus find protection within the cactus.

Eggs appear to be the most vulnerable stage in the *C. cactorum* life cycle. Eggsticks of *C. cactorum* take approximately one month to hatch in the field**,** and are afforded little protection by the cladodes and spines from prevailing environmental conditions such as high or low temperatures. Larvae are internal feeders and pupae are found in leaf litter on the ground. The purpose of this study was to evaluate the effects of high and low temperatures and exposure times on *C. cactorum* egg development and hatch. Knowledge of these temperature/time thresholds will become increasingly important as *C. cactorum* continues to expand its range in North America where average temperature variations are more extreme than in its current range. Furthermore, this information will be helpful in streamlining control strategies by enabling the focus of attention on areas where the moth is most likely to colonize and survive.

Materials and Methods

Eggsticks of *C. cactorum* were obtained from a colony maintained at the USDA-ARS Crop Protection and Management Unit laboratory in Tifton, GA**.** Larvae were reared on cladodes of *Opuntia ficus-indica* (L.) Miller inside rectangular plastic boxes that were maintained at 26°C ± 1°C, a photoperiod of 14:10 (L:D), and 70% RH. As larvae matured, cocoons were collected every 2-3 d from the containers. Pupae were extracted from the cocoons and placed in a screen cage (30.5 × 30.5 × 30.5 cm) where eclosion, mating, and oviposition occurred. Newly laid eggsticks (0-24 h old) were collected daily and transported in a small cooler (temperature approximately 4°C) to the USDA-ARS Center for Medical, Agricultural, and Veterinary Entomology laboratory in Tallahassee, FL, where the studies were conducted. The number of eggs per eggstick was determined under a dissecting microscope. Individual eggsticks were placed in a 30-ml plastic cup with a cardboard lid (Jet Plastica, Hatfield, PA).

Low Temperature Effect Studies

Different aged eggsticks (1, 7, and 14 d) were exposed to several treatment temperatures for various lengths of time and assessed for egg hatch. Eggsticks aged for seven and 14 d were held at the control temperature prior to exposure to treatment temperatures. Ten replicates (1 eggstick = 1 replicate) were completed at each treatment temperature and exposure time. Treatment temperatures were -10, -5, 0, and 5°C, while exposure times were 1, 2, 3, 4, 5, 10, 20, 40, and 60 d (Table 1). Thermo-Forma growth chambers (Thermo Electron Corporation, Marietta, OH) used for the different temperature treatments were programmed with a photoperiod of 0:24 (L:D) and 40-70% RH. Temperature and humidity inside each chamber were verified with HOBO data loggers (Onset Computer Co., Bourne, MA). After the predetermined length of exposure time at each treatment temperature, replicates were returned to the control chamber where they were checked daily for egg hatch. Date of first egg hatch was recorded and newly emerged larvae were carefully removed daily with a small brush. Eggsticks were inspected under a dissecting microscope to determine when egg hatch was completed. The percent egg hatch, the time and duration of egg hatch, and the time to complete egg hatch were calculated. Eggsticks that did not hatch after 60 d were discarded.

Developmental Studies

Ten replicates of 1-d-old eggsticks (1 eggstick = 1 replicate) were completed at each constant treatment temperature with a maximum exposure time of 60 d or until egg hatch. Eggs that did not hatch after 60 d were discarded. Treatment temperatures were 10, 15, 20, 25, 35, 40, and 50°C (Table 1), photoperiod 0:24 (L:D), and 40-70% RH. Replicates were inspected daily and the percent egg hatch, time and duration of egg hatch, and time to complete egg hatch were calculated as described for the low temperature effect study above. Data from a growth chamber set at 14:10 (L:D), 30°C, and 40-70% RH served as the control for both the low temperature effect study and the developmental study.

TABLE 1. LIST OF TREATMENT TEMPERATURES, EGG AGE AT SETUP, AND EXPOSURE TIMES; 10 REPLICATES COMPLETED FOR EACH COMBINATION.

Treatment temperature (°C)	Egg age at time of setup (d)	Number of days at treatment temperature	Number of days at 30°C control temperature
		Development Studies	
50	1	60	0
40	1	60	0
35	1	60	0
30 (control)	1	60	60
25	1	60	0
20	1	60	0
15	1	60	0
15	1	60	0
15	1	60	0
10	1	60	0
		Effect of Low Temperature Exposure Studies	
5	1	1	60
5	1	5	60
5	1	10	60
5	7	1	60
5	14	1	60
5	1	20	60
5	1	40	60
5	1	60	60
0	1	1	60
0	1	2	60
0	1	3	60
0	1	4	60
0	1	5	60
0	1	10	60
0	7	1	60
0	14	1	60
-5	1	1	60
-5	1	2	60
-5	1	3	60
-5	1	4	60
-5	1	5	60
-5	1	10	60
-5	7	1	60
-5	14	1	60
-10	1	1	60

Statistics

Data collected from developmental studies involving 1-d-old eggsticks held at constant treatment temperatures were analyzed by a two-factor analysis of variance (ANOVA), with treatment temperature and exposure time as sources of variation (PROC ANOVA and PROC GLM) (SAS Institute 1989). Data collected from low temperature effect studies where 1-d-old eggsticks were exposed to treatment temperatures for a prescribed exposure time and then returned to control conditions were analyzed by ANOVA and regression analysis, with exposure time and treatment temperature as sources of variation (PROC ANOVA and PROC GLM) (SAS Institute 1989). Data collected from low temperature effect studies where eggsticks were aged for a prescribed period under control conditions, exposed to treatment temperatures for 24 h, and then returned to control conditions, were analyzed by a three-factor ANOVA and regression analysis, with exposure time, treatment temperature, and age as sources of variation (PROC ANOVA and PROC GLM) (SAS Institute 1989). Exposure time in the statistical model denotes the length of time (in

days) that the eggsticks were subjected to treatment temperatures. The statistical model included the following dependent variables: percent hatch of eggsticks, time (in days) to first egg hatch, mean days to egg hatch, and time (in days) to last egg hatch. Percent egg hatch was calculated by comparing the total number of neonates with the total number of eggs in the eggstick. All other dependent variables were calculated from the date of oviposition. When the statistical model indicated significant treatment effects and significant interactions, differences among means were separated by the Tukey-Kramer statistic ($P \leq 0.05$) for multiple comparisons. Data met the assumptions of ANOVA and were not transformed.

RESULTS

Low Temperature Effect Studies

Analysis of data obtained when 1-d-old eggsticks were exposed to treatment temperatures for different exposure times revealed a significant ($F = 4.71$; $df = 6, 150$; $P = 0.0002$) interaction between treatment temperature and exposure time for the mean number of days to first egg hatch, as well as a significant ($F = 19.28$; $df = 10, 219$; $P < 0.0001$) interaction between treatment temperature and exposure time for the mean percent hatch. Generally, with increasing exposure time for each treatment temperature, time to egg hatch increased while percent hatch decreased (Tables 2 and 3).

One-d-old eggsticks exposed to a treatment temperature of -10°C for 24 h did not hatch when returned to control conditions, indicating that -10°C is lethal to young eggsticks (Table 3). In addition, there was no egg hatch in 1-d-old eggsticks held at -5°C for 3 d. The percent egg hatch at all exposure time periods at treatment temperature -5°C were significantly lower than the control. At this temperature, exposure time sharply reduced the percent egg hatch as exposure time increased from 1 to 3 d and resulted in 0% egg hatch of 1-d-old eggsticks exposed for 4 d.

At 0°C and 5°C, percent egg hatch was not significantly reduced until exposure times were greater than 5 and 10 d, respectively. No egg hatch occurred at 0°C after 20 d exposure; no egg hatch occurred at 5°C after 40 d (Table 3). It also appeared that no egg development occurred at 0°C and 5°C, and the eggs that were exposed to these low temperatures essentially took that many extra days to hatch when returned to the control growth chamber, e.g., eggs took approximately 21 d to hatch at 30°C and 31 d to hatch (10 d longer) when they were exposed for 10 d at 5°C and then returned to the control chamber at 30°C (Table 2).

An analysis of exposure time on mean time to egg hatch and mean hatch percent across treatment temperatures showed that there were no sig-

TABLE 2. EFFECT OF TEMPERATURE AND EXPOSURE TIME ON TIME TO EGG HATCH FOR 1-D-OLD *CACTOBLASTIS CACTORUM* EGGSTICKS. FOR THE CONTROL TREATMENT (0 D EXPOSURE TIME), EGGSTICKS WERE MAINTAINED IN A GROWTH CHAMBER AT 30°C, 14:10 (L:D), AND 40-70% RH; AFTER COLD TEMPERATURE TREATMENTS, EGGSTICKS WERE PLACED IN THE CONTROL CHAMBER UNTIL FIRST EGG HATCH OR A MAXIMUM OF 60 D. TREATMENTS WHERE EGGS DID NOT HATCH ARE DENOTED BY "NH"; EXPOSURE TIMES THAT WERE NOT ASSAYED ARE DENOTED BY "—".

Treatment temperature (°C)	Exposure time at treatment temperature (days)										
	Control[2]	1	2	3	4	5	10	20	40		
	Mean days to first hatch (± S.D.)[1]										
-10	20.8 ±1.0 Aa	NH	—	—	—	—	—	—	—		
-5	20.8 ± 1.0 Aa	24.2 ± 2.4 Ba	23.8 ± 2.0 Ba	24.5 ± 0.7 Ba	NH	NH	NH	—	—		
0	20.8 ± 1.0 Aa	22.7 ± 0.5 Bab	23.5 ± 1.3 BCa	24.3 ± 0.6 CDa	25.7 ± 0.8 DE	27.1 ± 0.8 Ea	33.3 ± 1.0 Fa	NH	—		
5	20.8 ± 1.0 Aa	22.6 ± 0.5 Bb	—	—	—	27.5 ± 0.7 Ca	31.1 ± 0.4 Db	41.6 ± 0.2 E	NH		

[1]Means within each row followed by the same uppercase letter are not different ($P > 0.05$); means within each column followed by the same lowercase letter are not different ($P > 0.05$).
[2]Data from a single control at 30°C was used for comparison with all treatments.

TABLE 3. EFFECT OF TEMPERATURE AND EXPOSURE TIME ON PERCENT EGG HATCH OF 1-D-OLD *CACTOBLASTIS CACTORUM* EGGSTICKS. FOR THE CONTROL TREATMENT (0 D EXPOSURE TIME), EGGSTICKS WERE MAINTAINED IN A GROWTH CHAMBER AT 30°C, 14:10 (L:D), AND 40-70% RH; AFTER COLD TEMPERATURE TREATMENTS, EGGSTICKS WERE PLACED IN THE CONTROL CHAMBER UNTIL FIRST EGG HATCH OR A MAXIMUM OF 60 D. EXPOSURE TIMES THAT WERE NOT ASSAYED ARE DENOTED BY "—".

Treatment temperature (°C)	Exposure time at treatment temperature (d)									
	control[2]	1	2	3	4	5	10	20	30	40
	Mean percent egg hatch (± S.D.)[1]									
-10	94.8 ± 8.6 Aa	0	—	—	—	—	—	—	—	—
-5	94.8 ± 8.6 Aa	52.3 ± 33.4 Ba	6.6 ± 18.8 Ca	3.4 ± 9.4 Ca	0	0	0	—	—	—
0	94.8 ± 8.6 Aa	81.4 ± 14.2 ABa	66.6 ± 24.0 ABb	65.9 ± 24.3 ABb	51.8 ± 33.6 B	63.1 ± 34.2 ABa	14.7 ± 16.2 Ca	0	—	—
5	94.8 ± 8.6 Aa	80.1 ± 21.1 Aa	—	—	—	79.8 ± 13.8 Aa	82.9 ± 14.8 Ab	40.8 ± 21.0 B	0	

[1]Means within each row followed by the same uppercase letter are not different (P > 0.05); means within each column followed by the same lowercase letter are not different (P > 0.05).
[2]Data from a single control at 30°C was used for comparison with all treatments.

nificant differences between percent hatch of eggs held at -5°C, 0°C, and 5°C after 1 d of exposure. There also were no significant differences in mean percent hatch of eggs held at 0°C and 5°C after 5 d of exposure. However, the percent egg hatch significantly increased when eggs were held at 0°C rather than -5°C for both 2 and 3 d of exposure. Percent egg hatch significantly decreased for eggsticks held for 10 d exposure at 0°C when compared to 5°C. Eggs took significantly longer to hatch at colder temperatures when exposed for 1 d at treatment temperatures of -5°C compared to 5°C, and 10 d at 0°C compared to 5°C.

When the data for aged eggsticks were analyzed, there was a significant (F = 3.28; df = 2, 178; P = 0.0402) interaction between age (1, 7, or 14 d old) and exposure time (0 or 1 d) on the mean number days to hatch. However, there was no significant low temperature effect (-5°, 0°, or 5°C), therefore data from all temperature treatments were pooled. For each eggstick age, exposure to low temperature for 1 d significantly increased the mean time to egg hatch when compared to the control (exposure time of 0 d) (Table 4).

There were significant (F = 6.64; df = 2, 179; P = 0.0017) interactions between temperature and exposure time, and age and exposure time (F = 4.28; df = 2, 179; P = 0.0154) on the percent hatch of eggsticks aged for 1, 7, and 14 d. Analysis of the temperature/exposure time interaction reveals that at -5°C, 1 d of exposure significantly decreased percent egg hatch compared to the control (0 d of exposure). Additionally, 1 d of exposure at -5°C significantly reduced egg hatch from that observed at 0°C and 5°C for the same exposure time (Table 5). Analysis of the egg age/exposure time

TABLE 4. EFFECT OF EGG AGE AND EXPOSURE TO LOW TEMPERATURE ON TIME TO FIRST EGG HATCH OF *CACTOBLASTIS CACTORUM* EGGSTICKS. EGGS WERE HELD IN A GROWTH CHAMBER AT 30°C, 14:10 (L:D), AND 40-70% RH; AFTER EGGS WERE EXPOSED TO TREATMENT TEMPERATURES THEY WERE RETURNED TO THE CONTROL CHAMBER UNTIL HATCH.

Egg age (d)	Time to egg hatch (d ± S.D.)[1]	
	Control (30°C)[2]	24 h exposure to low temperature[3]
1	20.8 ± 1.0 Aa	23.2 ± 1.5 Ba
7	20.8 ± 1.0 Aa	22.4 ± 0.4 Bb
14	20.8 ± 1.0 Aa	22.5 ± 0.4 Bab

[1]Means within each row followed by the same uppercase letter are not different (P > 0.05); means within each column followed by the same lowercase letter are not different (P > 0.05).
[2]Data from a single control was used for comparison with all treatments.
[3]Statistical analysis indicated no effect due to different low temperatures (-5°C, 0°C and 5°C) and as a result data were pooled across all temperature treatments.

TABLE 5. EFFECT OF EGG AGE AND EXPOSURE TO LOW TEMPERATURE ON PERCENT HATCH OF *CACTOBLASTIS CACTORUM* EGGSTICKS. EGGS WERE HELD IN A GROWTH CHAMBER AT 30°C, 14:10 (L:D), AND 40-70% RH; AFTER EGGS WERE EXPOSED TO TREATMENT TEMPERATURES THEY WERE RETURNED TO THE CONTROL CHAMBER UNTIL HATCH.

	Percent egg hatch (% ± S.D.)[1]					
	Treatment temperature (°C)			Egg age (d)		
Exposure time (d)	-5	0	5	1	7	14
control[2]	94.8 ± 8.3 Aa	94.8 ± 8.3 Aa	94.8 ± 8.3 Aa	94.8 ± 8.3 Aa	94.8 ± 8.3 Aa	94.8 ± 8.3 Aa
1	65.2 ± 28.6 Ab	86.3 ± 15.6 Ba	83.0 ± 24.0 Ba	71.3 ± 27.1 Ab	74.8 ± 26.2 Ab	88.5 ± 17.6 Ba

[1]Means within each row for a given variable (Treatment temperature or Egg age) followed by the same uppercase letter are not different ($P > 0.05$); means within each column followed by the same lowercase letter are not different ($P > 0.05$).
[2]Data from a single control at 30°C was used for comparison with all treatments.

interaction (Table 5) shows that 1- and 7-d-old eggsticks had significantly lower percent hatch when compared to the control, but 14-d-old eggsticks were not significantly different from the control. Additionally, 14-d-old eggsticks had a significantly higher percent hatch when compared to 1- and 7-d-old eggsticks after 1 d of exposure to low temperatures. However, at treatment temperatures of 0°C and 5°C there were no significant difference in percent egg hatch when compared to the control.

Developmental studies

One-d-old eggsticks of *C. cactorum* exposed to constant treatment temperatures failed to hatch at temperatures ≤15°C or ≥35°C and appeared to be desiccated. The highest percent hatch and shortest time to first egg hatch was obtained at 30°C (Table 2). At 30°C, all eggs hatched within 4 d of the initial hatch, with >50% occurring on the first d; while at 20°C, hatch duration was prolonged over a 9 d period with the highest number emerging on d 2 (Table 6).

DISCUSSION

To predict how far an invasive pest species will extend its range or how an existing species range will respond to climate change, it is important to understand what factors limit the range of that particular species (Baskauf & McCauley 2001). According to Pemberton (1995), Carpenter et al. (2001a), and Mahr (2001), it is likely that the geographical range of *C. cactorum* in the United States will be limited by environmental factors, such as temperature and photoperiod, rather than by host availability. North American *Opuntia* species have a broad geographical range and are tolerant of temperatures as low as -30°C and as high as 45°C (Carpenter et al. 2001b). Larvae of *C. cactorum* are polyphagous, feeding on nearly all *Opuntia* species tested to date (Stiling 2002). According to Hoffmann & Blows (1994) and Baskauf & McCauley (2001), when climate directly influences the extent of a species' range, limiting factors such as temperature may be fairly easily identified by testing whether the resistance of susceptible stages to abiotic stresses (such as extreme temperatures) matches the level of stress at the range limit.

This study evaluated the effect of various treatment temperatures on the percent egg hatch and time to first egg hatch of 1-d-old and aged *C. cactorum* eggsticks under laboratory conditions. The results obtained from the constant treatment temperatures show that there was no egg development at 15°C and 35°C. These results suggest that the lower and upper temperature thresholds for *C. cactorum* egg development would be 20°C and 30°C, respectively. However, the validity of

TABLE 6. PERCENT HATCH OF 1-D-OLD *CACTOBLASTIS CACTORUM* EGGS HELD AT CONSTANT TEMPERATURE FOR A MAXIMUM OF 60 D. TREATMENTS WHERE NO EGGS HATCHED ARE DENOTED BY "NH".

		Total number of days during which egg hatch occurred									
		1	2	3	4	5	6	7	8	9	
Temperature (°C)	Days to 1st hatch	Percent hatch per day									Total hatch (%)
15	NH										0
20	40	15	43	22	5	1	1	1	1	1	90
25	26	32	22	17	10	10	1				92
30	20	54	33	7	2						96
35	NH										0
40	NH										0
50	NH										0

such a conclusion would be suspect based on the inability of the growth chambers utilized in this study to maintain constant temperatures. Analysis of temperature data obtained from data loggers placed inside the growth chambers revealed that temperature within the chambers fluctuated between ±2.5°C of a prescribed constant temperature. As a result, eggsticks held at constant treatment temperatures of 15°C and 35°C were periodically exposed to lower and higher temperatures (12.5°C and 37.5°C, respectively). It is possible that the eggsticks were killed by periodic exposure to the temperature extremes above and below the treatment temperatures. In order to accurately determine the developmental threshold of *C. cactorum* eggs, this study should be repeated utilizing growth chambers with a narrower range of temperature fluctuations. The highest percent egg hatch and shortest time to egg hatch obtained in this study was observed at 30°C, suggesting that this temperature was closest to the optimal temperature required for *C. cactorum* egg development. At treatment temperatures of 20°C, eggsticks required twice as much time to hatch and had significantly lower percent egg hatch. The longer period required for neonate emergence at 20°C could be detrimental to neonate survival under field conditions. Entry into the cactus pad is thought to be achieved by the neonates chewing gregariously on the same spot in order to penetrate the cuticle and/or overcome the plants defenses (Pettey 1948). As such, when the period of emergence is staggered, as occurs at 20°C, there may be too few neonates to successfully enter the cactus pad, resulting in increased mortality due to predation or eventual desiccation of the young larvae.

Percent egg hatch for 1-d-old eggsticks held at low temperatures and returned to control conditions showed an inverse relationship with the length of exposure time at the low temperature. The longer eggsticks were held at the low temperature, the lower the percent egg hatch. At -5°C, percent egg hatch was low after 1 d and was further reduced until no eggs hatched at 4 d of exposure time. At -10°C, 1-d-old eggsticks did not survive even after 1 d of exposure time. These results suggest that 1-d-old eggsticks are highly susceptible to temperatures below 0°C and that significant mortality can be expected if 1-d-old eggsticks are exposed to below freezing temperatures in the field. At the 5°C treatment temperature, percent egg hatch was not significantly different from that observed in the control until exposure time reached 20 d. In addition, no egg hatch occurred when eggsticks were exposed to 5°C for 40 d. Time to egg hatch showed a direct relationship with exposure time. Longer times were required for egg hatch as exposure time to low treatment temperatures was increased. Eggsticks required twice the number of days to hatch as compared to the control when they experienced 20 d of exposure to 5°C.

Eggsticks aged for 7 and 14 d before treatment generally had higher percent egg hatch when compared to 1-d-old eggsticks exposed to similar temperature regimes. This would suggest that older eggsticks are less susceptible to the effects of low temperature under laboratory conditions. However, additional studies are needed to determine if these results would be similar under field conditions.

The process of dispersal is a key feature in the success of most invasive species. The ability of a species to direct itself or its offspring to favorable new habitats is a prerequisite for attaining widespread ecological dominance (Krushelnycky et al. 2003). As such, understanding factors such as the effect of temperature on rate of development that ultimately influences the distribution and abundance of an insect is a fundamental issue of insect ecology (Andrewartha & Birch 1954) and is a practical concern with insects like *C. cactorum* that produce environmental and economic damage (Baskauf 2003).

Data presented in this study offer valuable developmental information for *C. cactorum* egg-

sticks under laboratory conditions and provide a basis for future research projects designed to gain a greater understanding of the development of *C. cactorum* under laboratory and field conditions. This information will become increasingly important as *C. cactorum* continues to colonize new geographical regions. Many species with ranges that extend over large geographic areas show regional adaptations to climate and differentiate to the extent that separate populations are considered ecotypes (Flint 1980). At this point it is unknown whether such a scenario will occur with *C. cactorum* in North America, but, if it does, such a situation will have a significant impact on future management strategies of this invasive species.

Acknowledgments

We thank the staff at USDA-ARS-CMAVE in Tallahassee, FL, especially Nathan Herrick, John Mass, and Carla Evans, for assistance with monitoring experiments. We also thank Susan Drawdy, Robert Caldwell, and Robert Giddens at USDA-ARS-CPMRU, in Tifton, GA, for providing technical assistance and eggsticks from their colony of *C. cactorum*, and Richard Layton, University of Georgia, for assistance with data analysis. This research was supported by grants to Florida A&M University from USDA-APHIS and USDA-CSREES. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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