

# Thermal Requirements for Development of *Diaprepes abbreviatus* (Coleoptera: Curculionidae)

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**ABSTRACT** The root weevil *Diaprepes abbreviatus* (L.) was reared on artificial diet under controlled conditions of temperature and humidity. The lower thermal threshold for development of neonate larvae was estimated to be 15°C. The growth rate of neonate larvae increased exponentially with increasing temperature up to 30°C. The growth rate of later instars, however, was suppressed at 30°C and mortality was higher than that of larvae reared at 26°C. Larvae reared as late instars only (>56 d old), or continuously at 30°C, had increased mortality and produced smaller adults than larvae reared at 22 and 26°C. Larvae reared as late instars only (>56 d) or continuously at 22°C had similar survival rates compared with those reared at 26°C, and they emerged as larger adults compared with larvae reared at 26 or 30°C. The time required for development from neonate to pupation was  $125 \pm 3$  d (mean  $\pm$  SEM,  $n = 38$ ) at 26°C. Duration of the pupal stage was inversely proportional to temperature between 22 and 30°C. Pupal mortality was higher at 30°C than at 22 or 26°C. The total time required for a single generation from oviposition to adult emergence was estimated to be 154 d at 26°C and adequate humidity. Cumulative mean air and soil temperatures and rainfall for a location in central Florida were analyzed and presented for the period October 1991 through January 1999.

**KEY WORDS** *Diaprepes abbreviatus*, citrus, temperature, developmental rate, pupation

THE ROOT WEEVIL *Diaprepes abbreviatus* (L.) was first discovered on the mainland United States at Apopka, FL, in 1964 (Woodruff 1964). Since then, it has spread throughout central and southern Florida where it has become a key pest of citrus and ornamental plants. It is now conservatively estimated to cause losses in excess of \$75 million yearly to citrus growers in 20 Florida counties on >66,000 hectares (*Diaprepes* Task Force 1995). Adult *D. abbreviatus* feed on leaves of many plant species in addition to citrus, including crops such as cassava, cotton, peppers, potatoes, sugar cane, and sweet potatoes. However, defoliation by adults is of minor importance compared with the damage caused by larval feeding on roots. Females oviposit by cementing eggs between leaves; neonates fall to the ground and enter the soil. The larvae of *D. abbreviatus* burrow through the soil, feeding on progressively larger roots as they grow. Girdling of structural roots or the root crown can kill mature trees. In addition to direct damage, larval feeding provides infection sites for plant pathogens, particularly *Phytophthora* spp., that contribute to tree mortality and reductions in yield (Rogers et al. 1996).

Despite its economic importance, the developmental biology of this species has been little studied since the 1930s. Wolcott (1933, 1934, 1936) described larval and pupal development under minimally controlled

conditions. He estimated larval development as 300 d, concluded that an obligate diapause period occurred before pupation, and speculated that adults remained in the pupal chamber in the soil for weeks or months and emerged in response to rainfall. Recent work has shown that larval development can be completed in as little as 126 d (Lapointe and Shapiro 1999).

A continuous laboratory colony of *D. abbreviatus* has been maintained at the U.S. Horticultural Research Lab at Orlando, FL, since 1992. However, carefully controlled experiments to determine parameters of development in response to humidity and temperature have been lacking. Recently, this laboratory initiated a series of studies to address these questions. Lapointe and Shapiro (1999) determined the optimal range of soil moisture content for pupation of *D. abbreviatus* reared as larvae on artificial diet and transferred to soil. Here I report the results of trials designed to describe larval and pupal development under conditions of constant and varying temperature regimes on artificial diet. Soil temperature and rainfall data for a 7-yr period are presented as a reference and to indicate the range of temperatures larvae are subjected to in the field at one location in central Florida.

## Materials and Methods

**Temperature and Rainfall.** Soil temperatures and rainfall were logged from a University of Florida weather station maintained at the A.H. Whitmore U.S. Horticultural Research Laboratory Foundation Farm

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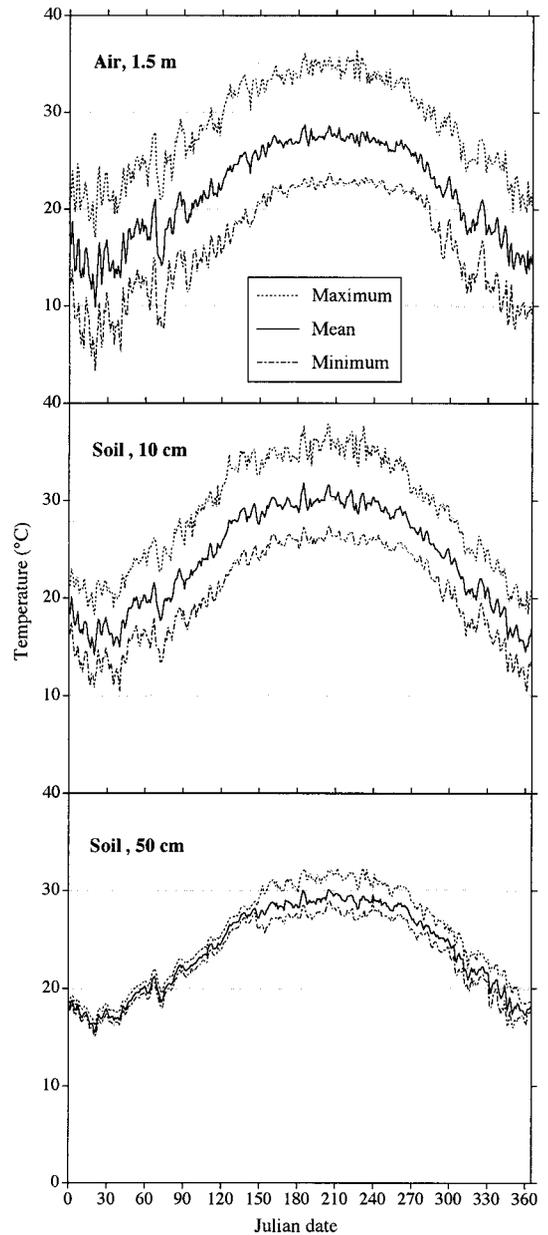
**Table 1.** Mean ( $\pm$ SEM) fresh weight and mortality of neonate *D. abbreviatus* larvae reared for 14 d on artificial diet at eight constant temperatures

°C	Wt, mg	n	% mortality
12	0.100 $\pm$ 0.004	10	100
15	0.293 $\pm$ 0.034	84	56
19	0.246 $\pm$ 0.019	51	15
21	0.759 $\pm$ 0.140	49	18
22	0.819 $\pm$ 0.144	47	22
26	2.462 $\pm$ 0.162	56	7
30	7.860 $\pm$ 0.486	52	13
34	0.260 $\pm$ 0.044	9	85

at Leesburg, Lake County, central Florida. Soil temperatures were collected at depths of 10 and 50 cm beneath a weed-free sandy soil in full sun. Temperatures were logged every minute over >7 yr. Rainfall was recorded daily during the same period. Average daily minimum, maximum, and mean temperatures, and mean weekly rainfall were calculated ( $n = 7$  for each date) and graphed for the period from 2 October 1991 through 20 January 1999.

**Neonate Development.** Male and female adult *D. abbreviatus* were obtained from a laboratory colony maintained by the U.S. Horticultural Research Laboratory, Orlando, FL. These were caged (20 pairs per cage) on citrus foliage and provided with strips of wax paper for oviposition (Wolcott 1933). Eggs were collected within 8 h of oviposition and placed in plastic vials in temperature-controlled incubators with a photoperiod of 12:12 (L:D) h. Vials were misted with sterile water periodically to avoid desiccation of the eggs. To determine the weight of newly hatched neonates, 10 replicates of 50 neonates each were weighed and the mean weight per neonate was calculated. Individual neonate larvae were then placed in diet cups (PC100 30 ml cups and lids, Jet Plastica, Harrisburg, PA) containing a commercially prepared insect diet (Product No. F1675, Bio-Serv, Frenchtown, NJ) as previously described (Beavers 1982, Lapointe and Shapiro 1999). Larvae in diet cups were kept in plastic bags to prevent desiccation of the diet and placed in a dark growth chamber (24 d) at one of eight constant temperatures—12, 15, 19, 22, 22, 26, 30, and 34°C. Larvae were removed, counted, and weighed after 14 d.

**Larval Development.** Individual neonate larvae were placed on artificial diet as described above. Diet cups containing larvae were placed in trays and held in plastic bags to prevent desiccation. Moisture content of the diet was 70% by weight at infestation of the cups. Water content of diet cups after 28 d was checked by drying the diet in an analytical oven at 60°C for >3 d. Water content of the diet moisture over a 1-mo period declined by 4% but remained within the range required for rapid development (Lapointe and Shapiro 1999). Larvae were placed in incubators at an initial temperature (T1). After 46 d (trial 1) or 28 d (trial 2), larvae were weighed and transferred to fresh diet and placed at a new temperature (T2). After an additional 28 d, larvae were again weighed, placed on



**Fig. 1.** Minimum, maximum, and mean daily air and soil temperatures at 10 and 50 cm, Leesburg, FL. Data are daily averages for 1991–1998.

fresh diet and placed at a third temperature (T3) until adults emerged. Subsequent to transfer to T3, larvae were weighed every 28 d and transferred to fresh diet to maintain optimal moisture conditions. Temperature treatments (T1–T2–T3) were 22–22–22, 26–26–26, 30–30–30, 22–26–30, and 30–26–22. The experiment was repeated: trial 1 was initiated on 20 November 1997; trial 2 began on 16 December 1997. An electrical outage in early December 1997 resulted in higher temperatures in the incubators for 2 d during the early

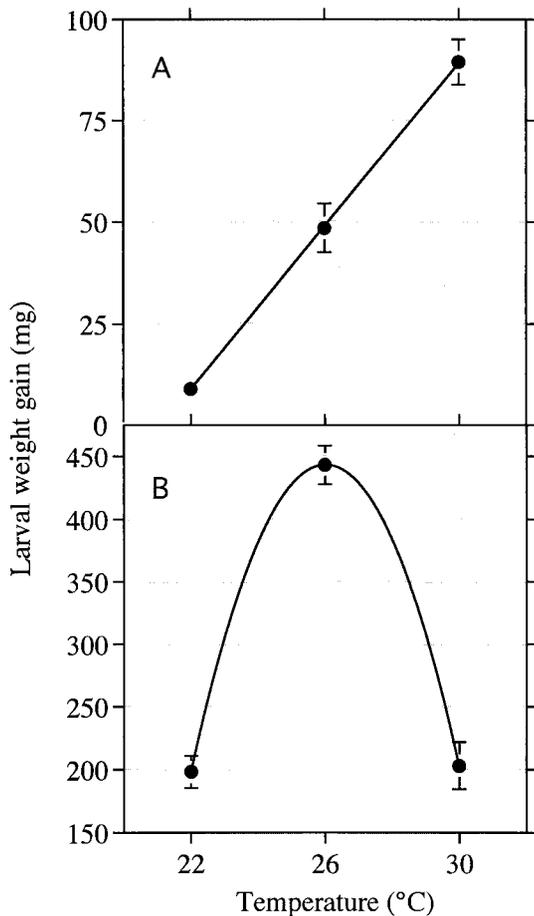


Fig. 2. Weight (FW  $\pm$  SEM) gained by larval *D. abbreviatus* reared individually on artificial diet at three constant temperatures during the first 28 d of development (A) and during the period between 28 and 56 d (B).

stages of trial 1. This did not result in larval mortality, and the trial was continued but repeated (trial 2).

**Pupation and Adult Emergence.** Diet cups were checked daily for pupae. Pupae were held at the same temperatures as the respective larval treatment (T3) until adults emerged. Duration of the pupal stage was recorded and adults were weighed upon emergence.

**Statistical Analysis.** The effect of temperature treatments on duration of larval and pupal stadia in days and degree-days and larval weights were analyzed by analysis of variance (ANOVA) as a completely randomized design. Duration in degree-days was calculated by multiplying the number of days at a given temperature by the number of degrees the daily temperature was in excess of the lower thermal limit (15°C). No weight gain was detected for larvae reared at 12°C and all died during the course of the 2-wk trial. A threshold of 15°C was used based on 50% mortality of neonate larvae reared at that temperature and because weight gain was very small (Table 1). Where appropriate, means were compared by the Tukey hon-

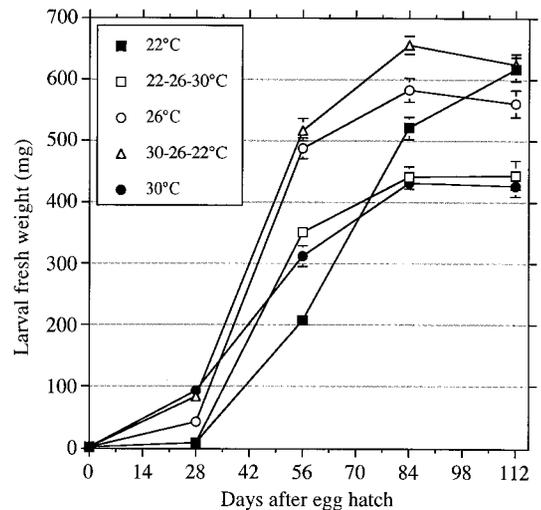


Fig. 3. Temporal pattern of larval growth (weight) for *D. abbreviatus* reared individually on artificial diet at five temperature treatments.

estly significant differences test (Abacus Concepts 1996).

## Results

**Temperature and Rainfall.** The daily mean air temperature (grand mean of daily means over 7 yr) at Leesburg, FL, fluctuated between a low of 9.9 and a high of 28.7°C with an overall mean ( $\pm$ SEM,  $n = 365$ ) of  $21.7 \pm 0.3^\circ\text{C}$  (Fig. 1). Daily mean soil temperature over the same period at 10 cm fluctuated between 9.9 and 28.7°C with an overall mean of  $24.1 \pm 0.3^\circ\text{C}$ . At 50 cm, daily mean soil temperature fluctuated between 15.5 and 30.1°C with an overall mean of  $24.0 \pm 0.2^\circ\text{C}$ . At 50 cm, temperatures were similar to those at 10 cm but less variable (Fig. 1). Mean weekly rainfall over the 7-yr period fluctuated between 0.32 and 4.97 cm. Highest rainfall (>14 cm/mo) occurred during the months of June through September; April and November were the driest months (<5 cm/mo).

**Neonate Development.** The mean weight of newly hatched neonates (24 h old) was  $100.4 \pm 4.3 \mu\text{g}$  ( $n = 10$ ). When placed on diet at 12°C, neonate mortality was high (>90%) and none showed detectable weight gain. At higher temperatures, larval fresh weight gain over 14 d increased exponentially with increasing temperature up to 30°C according to the relationship  $y = 0.006 \times 10^{0.101x}$  ( $r^2 = 0.95$ ) where  $y$  is larval weight (mg) and  $x$  is temperature (°C). Mortality was high (85%) at 34°C and weight gain of surviving larvae was very low (Table 1). At 34°C, 33% of the larvae were not recovered from the diet cups; they died and decomposed before the end of the 14-d incubation period. Only nine larvae (15%) were recovered alive and another 31 were recovered dead. Mortality of neonates was 56% at 15°C compared with 7% at 26°C (Table 1). Because neonate mortality exceeded 50%,

**Table 2.** Mean ( $\pm$ SEM) duration and mortality of larval stages of *D. abbreviatus* reared on artificial diet at different conditions of constant and varying temperature

°C	Larval period			% mortality
	Duration (d)	n	DD (°C - d > 15°C)	
		Trial 1		
26	106.4 $\pm$ 2.5a	31	1,170.6 $\pm$ 27.7a	11
22-26-30	132.5 $\pm$ 5.4b	29	1,507.8 $\pm$ 80.3b	17
30-26-22	134.1 $\pm$ 4.2b	33	1,418.6 $\pm$ 29.2b	13
30	140.3 $\pm$ 7.9bc	24	2,103.8 $\pm$ 118.4c	27
22	157.1 $\pm$ 5.0c	28	1,100.0 $\pm$ 35.0a	11
		Trial 2		
26	125.1 $\pm$ 3.1a	38	1,376.5 $\pm$ 34.6ab	0
30	143.8 $\pm$ 10.0ab	12	2,157.5 $\pm$ 149.9c	35
22-26-30	158.0 $\pm$ 10.4bc	15	2,034.0 $\pm$ 155.4c	50
30-26-22	163.8 $\pm$ 3.9bc	35	1,482.8 $\pm$ 27.5b	3
22	175.1 $\pm$ 3.1c	40	1,225.7 $\pm$ 21.5a	0

Means within columns followed by the same letter are not significantly different ( $\alpha = 0.05$ , Tukey HSD).

15°C was used as the lower thermal limit for the purpose of calculating degree-days.

**Larval Development.** When measured at 28 d after egg hatch, rate of larval growth was linearly related to temperature (Fig. 2A) within the range of 22–30°C. However, during the second month of larval growth (28–56 d), the rate of growth at 30°C declined relative to that at 26°C and was equivalent to the rate of growth at 22°C (Fig. 2B). Duration of larval stadia differed between trials 1 and 2, probably because of the brief power outage during trial 1. For this reason, data from trial 2 are probably more precise. Nevertheless, the data from the two trials are similar in that larval development at constant temperatures was fastest at 26°C and slowest at 22°C. Larval mortality, especially in trial 2, was highest at constant 30°C and increasing temperature (22-26-30°C) (Table 2). Although development was slower at constant 22°C compared with that at constant 26°C, larval mortality was low (Table 4), and larvae reared at constant 22°C or decreasing temperature (30-26-22°C) gained more weight (Fig. 3) and produced heavier adults than those reared at constant 26°C (Table 4).

**Pupation and Adult Emergence.** The temperature regime experienced during larval development had no effect on the duration of the pupal stadium ( $P > 0.1$ , ANOVA). The duration of the pupal stage was in-

versely proportional to temperature (T3). There was a slight effect of trial on duration of the pupal stage ( $P = 0.03$ , ANOVA) and there was a significant interaction between trial and temperature (T3) ( $P < 0.01$ ). Therefore, results of trials 1 and 2 are presented separately (Table 3). In both trials, the rate of pupal development was directly proportional to temperature, decreasing in trial 2 from 35 d at 22°C to 14 d at 30°C. Mortality during the pupal stage was negligible at 22 and 26°C, but increased at 30°C to 23 and 44% in trials 1 and 2, respectively.

Linear extrapolation of the relationship between developmental rate and temperature ( $y = 0.0045x - 0.0685$ ) yielded a lower thermal threshold for pupal development of 15.2°C. In trial 1, there was no difference in degree-days required for pupal development at the three temperatures tested (Table 3, ANOVA). In trial 2, the number of degree-days required for completion of the pupal stage at 30°C was significantly smaller compared with the other two temperatures ( $P < 0.01$ , ANOVA). However, given the high mortality (44%) at this treatment and the consequently smaller sample size (16), this difference was ignored to calculate the mean degree-days for pupation. The overall mean  $\pm$  SEM required for pupal development was  $233.6 \pm 2.2$  DD ( $n = 305$ ).

**Table 3.** Mean ( $\pm$ SEM) duration of and mortality during pupal stage of *D. abbreviatus* at three constant temperatures when reared on artificial diet

°C	Pupal stage			% mortality
	Duration (d)	n	DD (°C - d > 15°C)	
		Trial 1		
22	32.6 $\pm$ 0.6a	73	228.1 $\pm$ 3.9a	3
26	19.5 $\pm$ 0.5b	31	215.0 $\pm$ 5.8a	0
30	15.7 $\pm$ 0.5c	56	234.9 $\pm$ 6.9a	23
		Trial 2		
22	35.2 $\pm$ 0.7a	54	246.4 $\pm$ 4.7a	0
26	21.9 $\pm$ 0.4b	75	241.3 $\pm$ 4.0a	3
30	14.1 $\pm$ 0.5c	16	210.9 $\pm$ 7.7b	44

Means within columns followed by the same letter are not significantly different ( $\alpha = 0.05$ , Tukey HSD).

**Table 4.** Mean ( $\pm$ SEM) fresh weight of adults at emergence and mortality during immature stadia for *D. abbreviatus* reared at five temperature regimes on artificial diet

°C	Wt, mg	n	% mortality
22	366.8 $\pm$ 9.2a	52	3
30-26-22	352.0 $\pm$ 7.2a	58	8
26	321.0 $\pm$ 6.2b	69	7
22-26-30	278.1 $\pm$ 8.9c	31	46
30	244.3 $\pm$ 10.5c	28	35

Means followed by the same letter are not significantly different ( $\alpha = 0.05$ , Tukey HSD).

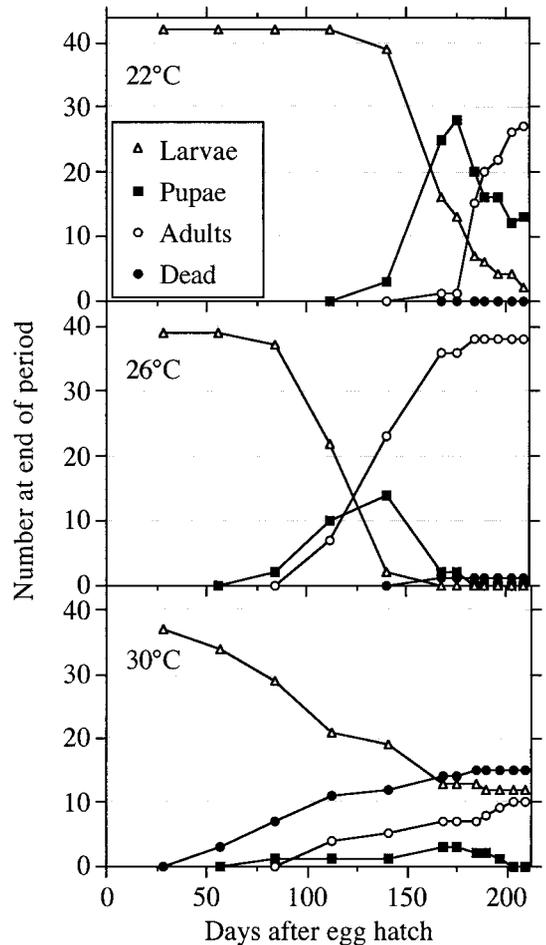
There was no effect of trial ( $P = 0.98$ , ANOVA), nor was there a significant interaction between trial and temperature ( $P = 0.11$ , ANOVA) on fresh weight of adults at emergence. Temperature had a highly significant effect on adult weight ( $P < 0.01$ , ANOVA). Adults weighed least at emergence when reared either at 30°C continuously or at 22-26-30°C. The largest adults emerged when larvae were reared either at 22°C continuously or at 30-26-22°C (Table 4).

Cumulative mortality (combined larval and pupal mortality) was high when insects were reared at 30°C continuously or at 22-26-30°C. The highest mortality occurred when the temperature experienced by late instars was 30°C (constant 30°C and 22-26-30°C). At constant 22°C, larvae took longer to develop to adult compared with larvae reared at constant 26°C (Table 4). Adult emergence took an average of 64 d longer at 22 than at 26°C, and 21 d longer at 30 than at 26°C (Fig. 4).

### Discussion

Conditions of humidity experienced by larvae and pupae were maintained constant throughout the experiments by holding diet cups in plastic bags and by replacing diet cups with fresh diet every month. This probably was responsible for low variance associated with mean development times and weights compared with previous studies.

For *D. abbreviatus*, there was a strong interaction between age of larvae and response to temperature. The developmental rate of neonates asymptotically approached zero as temperature decreased below 22°C; 15°C appears to be the lower thermal limit for neonates. Weight gain was exponentially related to temperature during the first 14 d after egg hatch. Subsequently, to 28 d, larval weight gain was linearly related to temperature in the range of 22–30°C. Finally, larval weight gain from 28 to 56 d after egg hatch at the same temperatures showed a strong reduction and increased mortality at 30°C (Fig. 2). The results indicate that growth of early instars is favored by high temperatures but late instars have a lower optimal temperature for development (26°C). For this reason, it may not be appropriate to use the lower thermal limit determined for neonates (15°C) for other life stages. However, linear extrapolation of pupal developmental rates resulted in a lower thermal limit for



**Fig. 4.** Age-specific survivorship of *D. abbreviatus* reared on artificial diet at three constant temperatures. Data for adults and dead (larvae and pupae) are cumulative.

pupation of 15.2°C, nearly identical to the threshold for neonates.

In the field, adult *D. abbreviatus* oviposit on leaves. Neonates fall to the ground, disperse, and begin to burrow in search of feeding sites. During this process, they may be exposed for varying periods to relatively high temperatures as demonstrated by the daily maxima for air and superficial soil temperatures at Leesburg (Fig. 1). Presumably, later instars, which occur at greater depths, are insulated from higher temperatures and temperature fluctuations.

Wolcott and Martorele (1943) observed an abundance of egg masses on sugar cane in Puerto Rico during May–June with a secondary peak in September–October. Few eggs were found after early December. In Florida, adults of *D. abbreviatus* can be found in the field throughout the year, with peaks often preceded by heavy rainfall (Beavers and Selhime 1986). Given the yearly mean soil temperature at Leesburg, FL, of 24°C, interpolating from the values in tables 2 and 3, and assuming a preoviposition period of

14 d (unpublished data), a single generation of *D. abbreviatus* would take 200 d or 28.5 wk. Although two generations per year may be possible under warmer soil conditions, this calculation may explain why no strong seasonal peak of abundance for adults has been observed in central Florida and why adults are observed in the field over several months.

In the study reported by Quintela et al. (1998), mean duration of the larval period of *D. abbreviatus* was  $153 \pm 28$  d and duration of the pupal stage was  $17 \pm 4$  d at 27°C. The duration of the larval stadia was 4–7 wk longer than reported here at 26°C (Table 2). Also, the results of Quintela et al. (1998) were variable as measured by coefficient of variation, *C* (standard deviation/mean) calculated here from their results: duration of larval stadia was 153 d (*C* = 108%), duration of pupal stage was 17 d (*C* = 59%), mean larval weight before pupation was 480 mg (*C* = 124%), and mean adult weight was 276 mg (*C* = 97%). Subsequent to that publication, Lapointe and Shapiro (1999) demonstrated the importance of humidity to development and pupation of *D. abbreviatus*. In that study, larval development was completed in  $126 \pm 2.3$  d (*C* = 13%). They showed that diet cups containing artificial diet used for rearing *D. abbreviatus* were subject to desiccation, especially over the long periods (4–5 mo) required for *D. abbreviatus* to complete development. In the experiments reported here, care was taken to avoid loss of moisture in the diet by sealing the cups in plastic bags and replacing the diet every 28 d. As a result, development was fast and synchronized: the larval period was 106 d in trial 1 (*C* = 13%) and 125 d in trial 2 (*C* = 15%); the pupal stage was 20 d in trial 1 (*C* = 14%) and 22 d in trial 2 (*C* = 16%). Similarly, fresh weight of adults was less variable in the current study where humidity was controlled than in the previous study (mean adult fresh weight at emergence at 26°C was 321 mg, *C* = 16%) (Table 4). These data show there is no obligate diapause as suggested by Wolcott (1934) and suggest that, exclusive of host plant effects, soil temperature and humidity alone determine developmental rate and the timing of adult emergence.

DuCharme (1971) showed that soil under shade of citrus trees in Florida was cooler and had a more uniform temperature than unshaded soil both in Lakeland fine sand (Lake Alfred, Polk County) and Parkwood soil (Ft. Pierce, St. Lucie County). The upper 15 cm were subject to large diurnal temperature fluctuations, influenced by shading and water saturation. At depths below 46 cm, temperature was similar in shaded and unshaded and little diurnal oscillation was detected. At 15 cm, the maximum daily temperatures in unshaded soil exceeded 30°C in the summer; in shaded soil, maximum daily values only reached a yearly high of approx. 26°C at Lake Alfred. Diurnal temperature fluctuations were not as great in Parkwood soil (Ft. Pierce) as in Lakeland soil. Summer high maximum temperatures at 15 cm were approx. 29 in unshaded and 24°C in shaded soils.

The rate of pupal development was directly proportional to temperature, requiring approximately twice as many days (15 d) to complete pupation at

22°C compared with 30°C (34 d). Mean daily winter soil temperatures in central Florida routinely fall below 20°C for 2–3 mo (Fig. 1). Additional trials would be required to determine accurately the lower thermal limit for pupal development and the effect of lower temperatures on pupal survival. It is not known when pupation occurs in the field. If adult emergence can be demonstrated by field-trapping to be synchronous, it may be worthwhile to determine the proximal stimulus for adult eclosion and emergence (Tauber et al. 1998). Teneral adult *D. abbreviatus* remain in the pupal cell for a variable period of time before emerging. Spring rains may trigger spring emergence whereas continuous high moisture in the soil may ensure continuous development over the summer months. In this context, management practices related to irrigation methods may affect the seasonal ecology of *D. abbreviatus*.

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