Temperature, Photoperiod, and Aggregation Effects on Development, Diapause, Reproduction, and Survival in *Corythucha cydoniae* (Heteroptera: Tingidae)[1]

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ABSTRACT *Corythucha cydoniae* (Fitch), the hawthorn lace bug, required an average of 55.6 - 18.5 days to complete development at temperatures ranging from 21 - 33°C. Nymphs emerged from eggs at 18°C but failed to develop further. Nymphal survival at 21°C was poor. Developmental thresholds for egg, nymphal, and total development were 13.3, 14.9, and 14.3°C, respectively. Thermal unit requirements for those stages were 162.9, 157.3, and 318.2 centigrade degree-days. Nymphal development was slightly accelerated by increasing the size of a cluster from one to three individuals at 24 but not at 27°C. Ovipositional rate was higher at 33 than 27°C, but total egg production was similar at both temperatures. Critical photoperiod for reproductive diapause was between 13:11 and 12:12 (L:D) at 24°C. Nymphal development was accelerated at short daylengths.

KEY WORDS Insecta, hawthorn lace bug, threshold, thermal unit requirements.

Corythucha cydoniae (Fitch), the hawthorn lace bug, is a widely distributed polyphagous pest of rosaceous plants and has few known natural enemies (Bailey 1951, Drake and Ruhoff 1965, Horn et al. 1979, Wheeler 1981, Neal and Douglass 1990). Plants are damaged when adults and gregarious nymphs feeding on the underside of the leaves produce initially small, chlorotic blotches that appear on the upper leaf surface. Severe infestation results in foliage with a bronzed or bleached appearance and early leaf abscission.

Oviposition and nymphal survival of hawthorn lace bug have been compared on resistant and susceptible species of *Cotoneaster* (Schultz and Coffelt 1987). Bailey (1951) determined that *C. cydoniae*, which overwinters as an adult, completes one generation in Massachusetts. Neal and Douglass (1990) reported that this species is trivoltine in Maryland. In addition to studies on voltinism, they reported the effect of three temperatures on longevity, fecundity, and development of the immature stages. They also showed that while adults and nymphs reared under a 14:10 (L:D) photoperiod did not diapause, nymphs reared under natural, declining light in a glasshouse produced reproductively

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diapausing adults. Neal et al. (1992) further examined the influence of photoperiod on diapause for this species determining sensitive stages and critical photoperiod for *C. cydoniae* in Maryland. While preimaginal stages were found to perceive and respond to diapause-inducing photoperiods, the adult was determined to be the ultimate sensitive stage.

Forecasting models based on heat accumulation units have been developed for several pests of landscape plants (reviewed in Raupp et al. 1992). Braman et al. (1992) reported a thermal unit model for predicting development of the azalea lace bug, *Stephanitis pyrioides* (Scott). Such methods for precisely predicting insect development are becoming more important with the increasing impetus for maximizing insect control through improved timing of application while minimizing pesticide use (Ascerno 1991).

Both photoperiod and temperature are known to influence developmental times and modify diapause induction, maintenance, and termination (Beck 1980, Tauber et al. 1986). Degree of aggregation also has been shown to influence survival and rate of development (Matsumoto 1989, 1990, Lawrence 1990). A more complete knowledge of each of these aspects will enhance our understanding of the seasonal dynamics of this species. The objective of our work, therefore, was to more closely define the influence of temperature, photoperiod, and group size on development and diapause in *C. cydoniae.* Data reported here further extend the range of existing information by providing thermal unit models for development.

Materials and Methods

A laboratory colony of *C. cydoniae* was initiated with adults collected from *Cotoneaster* sp. in Griffin, GA. The colony was maintained on greenhouse grown *Cotoneaster dammeri* C. K. Scheid. and was periodically supplemented with field collected individuals. Six wooden frame cages, one meter (l) × one meter (w) × one meter (h), covered with 32-mesh saran screen (Chicopee Co., Gainesville, GA) were used to house the colony and were kept on greenhouse benches under a 15:9 (L:D) photoperiod using sodium lamps.

Egg and nymphal development were compared at constant temperatures in environmental chambers (Percival Manufacturing Company, Boone, IA) at a photoperiod of 15:9 (L:D). Temperatures were 18, 21, 24, 27, 30, and 33 ± 1°C. Females were confined to cuttings of greenhouse-grown *C. dammeri* for 24 h in each respective temperature regime. Eggs deposited during that time were reared at each temperature and examined twice daily for eclosion. Nymphs were transferred and confined to new cuttings upon hatching as described in Braman et al. (1992) and were observed twice daily for molting as indicated by the presence of exuviae. Nymphs were supplied with additional plant material every 7 days.

Group size and effects were determined by following the same procedures as above except that nymphs were confined in 10 clusters each of 3, 5, or 10 individuals per cutting at 24°C and 3 individuals at 27°C. Survival and duration of total development of nymphs reared in clusters were compared to individuals reared singly. Plant material was changed every 7 days.

Differences in longevity, daily oviposition rate, preoviposition period, and total egg production were assessed by pairing newly-emerged individuals on cuttings of

C. dammeri and observing daily for eggs at 27 and 33°C. Adults were transferred daily to new cuttings.

Photoperiod effects on diapause and nymphal development were determined at constant 24°C. Duration of nymphal development was determined at daylengths of 10, 12, and 14 h. The relationship between daylength and incidence of diapause was examined by rearing individuals from egg to adult at 10, 12, 13, and 14-h photophases. Proportion of individuals ovipositing within 30 days of emergence as adults was compared among daylengths.

The relationship between constant temperatures and developmental rates along the linear portion of the developmental curves was established using least squares linear regression as described in Braman et al. (1984, 1985), Braman and Yeargan (1988), and Braman et al. (1992). Developmental times for nymphs reared at the same temperature but in different cluster sizes were subjected to analysis of variance with mean separation using least significant difference test (Sokal and Rohlf 1981).

Results and Discussion

Egg and Nymphal Development. Successful development occurred at temperatures ranging from 24 to 33°C (Fig. 1, Table 1). Eggs hatched at 18°C, but all except 1/54 nymphs died immediately. Only four nymphs of an original cohort of 59 individuals survived to the adult stage at 21°C. Nymphal survival when reared at the other four temperatures averaged 50.6%.

Duration of egg, nymphal, and total development in days ranged from 8.3 - 30.1, 10.2 - 29.3, and 18.5 - 55.6, respectively. Neal and Douglass (1990) determined that *C. cydoniae* in Maryland developed successfully at 20.6, 26.1, and 31.7°C. Egg and nymphal development in that study of 20.6°C required an average of 19 and 23.4 days, respectively. This represents a considerably shorter period of time than that required by *C. cydoniae* collected in Georgia as determined in the present study at 21°C; 26.5 and 29.3 days. Development reported by Neal and Douglass at 26.1 and 31.7°C was similar to that which occurred in the present study at temperatures between 24 and 33°C.

Estimated developmental thresholds for egg, nymphal, and complete development presented in Table 2 for *C. cydoniae* are higher than those previously determined for the azalea lace bug, *Stephanitis pyrioides* (Scott), which were 10.2, 12.2, and 11.2°C, respectively (Braman et al. 1992). Both species are serious pests of ornamentals in the eastern United States. Ericaceous plants are attacked by the immigrant species, *S. pyrioides,* which overwinters as an egg in the leaves of its evergreen hosts. *Corythucha cydoniae,* however, overwinters as an adult emerging in the spring to oviposit in the new leaves of its many deciduous host plants. Considerable variation may be found in response to temperature by other members of this genus. Stone and Waterson (1985), for example, considered 17.8°C to be the effective lower limit for development of *Corythucha morrilli* Osborn and Drake on guayule. The threshold for development of *Corythucha ciliata* (Say) eggs was determined to be about 12°C on *Platanus* sp. (Santini and Crovetti 1985). As mentioned previously, hawthorn lace bug was shown to be trivoltine in Maryland (Neal and Douglass 1990). Despite prolonged developmental rates and impaired survival at cool temperatures reported here, thermal unit

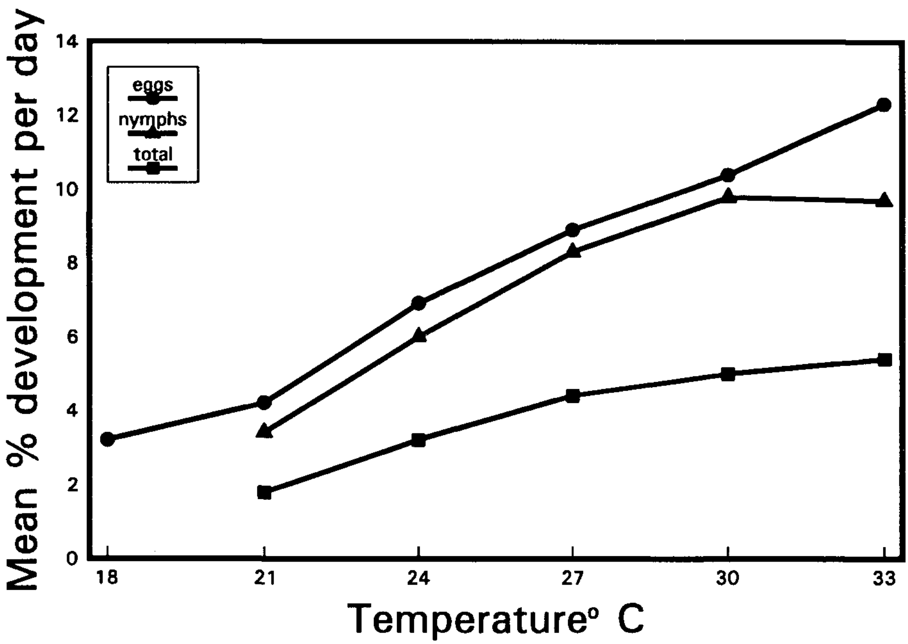

Fig. 1. Response of egg, nymphal, and combined stages of hawthorn lace bug to temperature.

requirements for complete development of *C. cydoniae* as determined in the present study (318.2 degree-days) suggest the potential for at least three generations in Georgia when compared to average yearly thermal accumulations for the central Georgia area.

Group size effects. Survival of nymphs was unaffected by cluster size ($P >$ 0.05, data not presented). An increase from one to three individuals per cutting resulted in reduced developmental time at 24 but not at 27°C (Table 3). Further increases in cluster size at 24°C resulted in similar (cluster of 5 individuals) or extended (cluster of 10 individuals) developmental times compared with that for single nymphs. Benefits of aggregation among insects often include enhanced survivorship and increased rate of development with beneficial effects becoming pronounced when larvae are supplied a less suitable food plant (Lawrence 1990, Matsumoto 1989, 1990). Feeding may have been facilitated by voluntary gregariousness of small cluster sizes. However, lace bugs in the largest cluster size (10) may have suffered from overcrowding.

Reproduction. Total fecundity for *C. cydoniae* did not differ when females were reared at different temperatures ($P > 0.05$, Table 4). Female longevity and, therefore, daily oviposition rate were influenced by temperature ($P < 0.05$, Table 4). Average fecundity determined in this study was considerably less than the 322

Table 1. Mean ± S. E. duration of development in days, and number of individuals completing each stage, of *C. cydoniae* on *Cotoneaster dammeri* cuttings.*

	Instar					Total		
Temp. °C	Egg	1	2	3	4	5	Nymphal	Total
18	30.7 ± 0.2 (54)	10.0 ± 0 (1)	ND†	ND	ND	ND	ND	ND
21	26.5 ± 0.4 (59)	6.9 ± 1.0 (20)	3.4 ± 0.2 (13)	4.9 ± 0.1 (9)	7.2 ± 0.6 (5)	7.9 ± 0.6 (4)	29.3 ± 0.4 (4)	55.6 ± 1.3 (4)
24	14.4 ± 0.1 (33)	3.2 ± 0.1 (28)	2.8 ± 0.1 (27)	2.9 ± 0.1 (27)	2.6 ± 0.1 (26)	4.8 ± 0.1 (25)	16.5 ± 0.2 (25)	30.9 ± 0.2 (25)
27	11.3 ± 0.1 (103)	2.1 ± 0.1 (57)	2.4 ± 0.1 (49)	1.9 ± 0.1 (41)	2.1 ± 0.1 (37)	3.3 ± 0.3 (33)	12.1 ± 0.2 (33)	22.8 ± 0.3 (33)
30	9.6 ± 0.1 (48)	2.1 ± 0.1 (27)	1.8 ± 0.1 (23)	1.8 ± 0.1 (22)	1.6 ± 0.1 (22)	2.8 ± 0.1 (21)	10.2 ± 0.1 (21)	19.8 ± 0.2 (21)
33	8.2 ± 0.1 (76)	2.2 ± 0.1 (55)	1.8 ± 0.1 (51)	1.6 ± 0.1 (44)	1.9 ± 0.1 (40)	2.7 ± 0.1 (35)	10.3 ± 0.1 (35)	18.5 ± 0.2 (35)

* Values in parentheses are number of individuals entering each stage.
† ND = no development occurred at this temperature.

Table 2. Linear thermal unit models, threshold temperatures (T_0), and mean thermal unit requirements (K) for development in degree days (DD) of each stage of *C. cydoniae*.

Developmental stage	Equation and r^2*	T_0, °C+	K,DD+
Egg	y = 0.0063t - 0.084 r^2 = 0.75	13.3	162.9
Instars			
First	y = 0.0429t - 0.700 r^2 = 0.40	16.3	27.1
Second	y = 0.0276t - 0.275 r^2 = 0.25	9.9	38.6
Third	y = 0.0487t - 0.797 r^2 = 0.31	16.4	22.3
Fourth	y = 0.624t - 1.120 r^2 = 0.27	17.9	19.2
Fifth	y = 0.304t - 0.493 r^2 = 0.22	16.2	37.4
Total nymphal	y = 0.0067t - 0.100 r^2 = 0.90	14.9	157.3
Complete	y = 0.0033t - 0.047 r^2 = 0.90	14.3	318.2

* y, reciprocal of mean development times; t, temperature, r^2, coefficient of correlation.

† T_0 and K for egg stage calculated for 18-33°C range, T_0 and K for nymphal and complete development calculated for 21-30°C range.

eggs per mated female on *Pyracantha coccinea* reported by Neal and Douglass (1990), comparing more closely with average egg production of 50.3 eggs produced by the congeneric species *C. juglandis* at 23.9° and 16:8 (L:D) photoperiod (Vogt and McPherson 1986) and the 21-43 eggs per female for *C. arcuata* (Say) (Connell and Beacher 1947) on white oak. Schultz and Coffelt (1987) examined oviposition and survival of *C. cydoniae* on 13 species or cultivars of *Cotoneaster*. Average egg production ranged from 47.4-146.1 depending on cultivar and was highest on *C. dammeri* 'Royal Beauty'. Oviposition on *C. dammeri* 'Lowfast' in that study averaged 86.1 eggs. The cultivar of *C. dammeri* used in the present study, 'Coral Beauty' is apparently more similar to 'Lowfast' than 'Royal Beauty' in suitability as a host for oviposition.

Table 3. Influence of cluster size on nymphal development.

Cluster size	n[1]	n[2]	Duration of development in days*
			24°C, 15:9 (L:D)
1	33	25	16.5 b
3	10	20	15.1 c
5	10	33	15.9 b
10	10	52	17.1 a
			27°C, 15:9 (L:D)
1	103	33	12.1 a
3	10	23	12.0 a

* Means followed by the same letter within a column and a temperature are not significantly different ($P > 0.05$), LSD.
n[1], Number of cohorts of each cluster size of first instars.
n[2], Number of individuals surviving to the adult stage.

Table 4. Influence of temperature on reproductive potential of *C. cydoniae* at 15:9 (L:D) photoperiod*

		Mean + S. E.			
Temp °C	N	preoviposition period (days)	female longevity (days)	no. eggs female/day	total no. eggs/female
27°C	24	5.6 ± 0.4 a	21.6 ± 0.9 a	1.9 ± 1.3 a	49.8 ± 6.4 a
33°C	15	4.9 ± 0.7 a	13.9 ± 1.0 b	3.4 ± 2.3 b	47.5 ± 8.3 a

* Means followed by the same letter within a column are not significantly different ($P > 0.05$), t-test.

Photoperiod. Incidence of reproductive diapause (Fig. 2) and duration of nymphal development (Table 5) were significantly influenced by photoperiod. The proportion of females that failed to oviposit within 30 days of emergence declined sharply between daylengths of 12 and 13 h. Neal et al. (1992) reported a critical daylength between 13 and 14 h for *C. cydoniae* at about 40° N latitude in Maryland. The decreasing nymphal developmental time observed in relation to decreasing daylength may serve to further synchronize the insects life cycle with the onset of unfavorable fall conditions (Tauber et al. 1986, Ruberson et al. 1991).

Understanding those aspects of the developmental and reproductive biology of the hawthorn lace bug in relation to temperature and photoperiod discussed here is essential to the development and implementation of information-based pest management strategies. Geographical differences in response to temperature and photoperiod often result in differences in threshold temperatures, thermal unit requirements for development, or critical daylength for diapause. These differences further serve to synchronize species having a broad geographic distribution with local climatic conditions. Hawthorn lace bug, a polyphagous North American species with a broad geographic range, appears to respond differently to low temperatures and photoperiod depending upon geographic locations of population, thus demonstrating this type of adaptation.

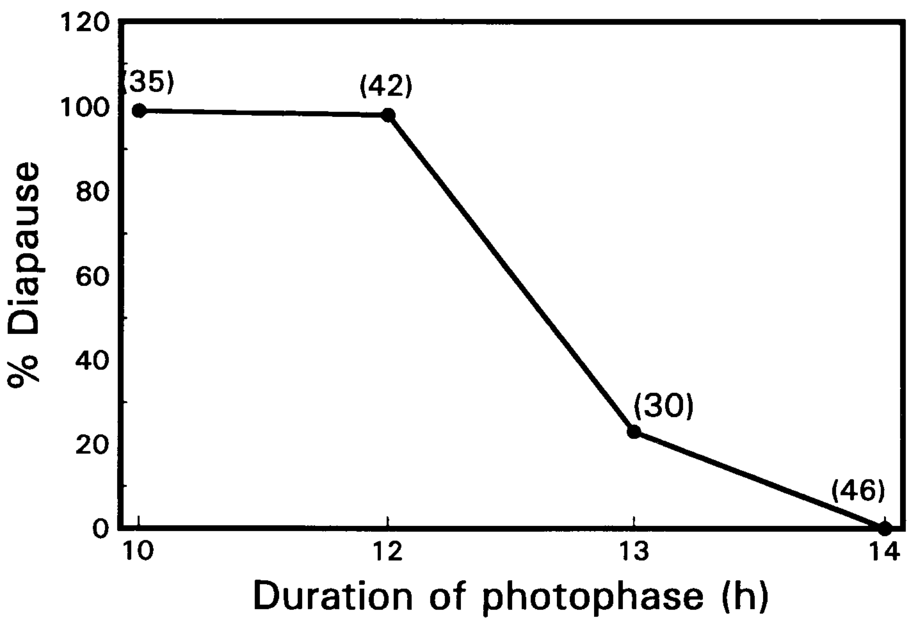

Fig. 2. Incidence of reproductive diapause of hawthorn lace bug in relation to daylength.

Table 5. Influence of photoperiod on nymphal development at 24°C.

Photoperiod (L:D)	Mean ± s.e. days to develop*	n
10:14	15.0 ± 0.1 a	21
12:12	16.1 ± 0.1 b	27
14:10	17.2 ± 0.1 c	23

* Means followed by different letters are significantly different ($P < 0.001$), LSD.

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