

Development and functional response of *Coelophora inaequalis* (Coleoptera: Coccinellidae) feeding on brown citrus aphid, *Toxoptera citricida* (Homoptera: Aphididae)

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- Abstract**
- 1 Development and survivorship of *Coelophora inaequalis* (F.) were evaluated in the laboratory on the brown citrus aphid, *Toxoptera citricida* (Kirkaldy) at 20 and 25 °C. *Coelophora inaequalis* could complete its life cycle feeding on *T. citricida* at these two temperatures. The developmental period from egg to adult was significantly longer at 20 °C (24.7 d) than at 25 °C (15.9 d). The survivorship of combined immature stages were higher at 25 °C (39.2%) than at 20 °C (34.3%).
 - 2 The effects of prey densities (4–64 aphids per leaf disk) on the functional responses of *C. inaequalis* fourth-instar larvae and female adults were investigated using grapefruit leaf disks over a 24-h period at 25 °C and a photoperiod of LD 14 : 10 h. Logistic regression analyses indicated that fourth-instar larvae and adults exhibited a type II functional response to aphid density. Fourth-instar larvae had a higher search rate (0.1305) than *C. inaequalis* female adults (0.0989). The handling time of fourth-instar larvae (30.4 min) was significantly longer than that of female adults (5.8 min). Collectively, *C. inaequalis* appears to be a promising biological control agent of *T. citricida* in the citrus groves.

Keywords *Coelophora inaequalis*, development, functional response, *Toxoptera citricida*.

Introduction

The brown citrus aphid *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae), is a newly introduced pest on citrus in the United States. The aphid is native to East Asia, but it has now colonized virtually all of the world's citrus production areas except the Mediterranean region and the remaining citrus producing states in the U.S.A. (Halbert *et al.*, 2000). It is one of the most damaging pests of citrus, primarily because it is an efficient vector of citrus tristeza virus (CTV) (Yokomi *et al.*, 1994). The rapid spread of CTV that killed tens of millions of trees grafted on sour orange (*Citrus aurantium* L.), rootstock in Brazil and Argentina in the 1930s and 1940s (Knorr & DuCharme, 1951) has been attributed to this aphid. Recently, studies showed that some CTV isolates can cause stem pitting regardless of rootstock (Bar-Joseph *et al.*, 1989), and can result in long-term debilitation that reduces yields of sweet orange and grapefruit by 5–45% (Yokomi & Tang, 1995).

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Since the introduction of brown citrus aphid in autumn 1995 in Florida, the biology and ecology of this insect have been well documented (Tsai, 1998; Michaud, 1999; Tang *et al.*, 1999; Tsai & Wang, 1999). However, the threat of CTV transmission by this aphid is unclear. Up to now, studies on biological control agents have included a coccinellid predator *Cycloneda sanguinea* L., a hymenopteran parasitoid *Lysiphlebia japonica* (Ashmead), and hyphomycete entomopathogens (Morales & Burandt, 1985; Deng & Tsai, 1998; Poprawski *et al.*, 1999). Michaud & Browning (1999) reported that a complex of large coccinellid species had the greatest potential to have an impact on brown citrus aphid populations in Puerto Rico.

Based on our observations, one of the most abundant ladybird species occurring in South Florida citrus groves is *Coelophora inaequalis* (F.) (unpublished data). However, no quantitative data on the relationship between *C. inaequalis* and the brown citrus aphid are available. Several studies have suggested that brown citrus aphid may be toxic to certain predators, or nutritionally inadequate for their successful development (Tao & Chiu, 1971; Morales & Burandt, 1985). The suitability of brown citrus aphid as prey must therefore be determined to

assess the capacity of *C. inaequalis* to maintain significant numbers in affected orchards. Understanding the development and functional response of a predator is important to the effectiveness of biological control of an insect pest (Juliano, 1993). Therefore, we evaluated the development and efficiency of adult and fourth-instar *C. inaequalis* as a predator of brown citrus aphid through functional response experiments.

Methods

Aphid and predator colonies

Toxoptera citricida used in this study were initiated by a single collection of wild aphids from a citrus tree on the campus of Broward Community College, Davie, Broward County, Florida. The colonies were maintained on potted grapefruit (*Citrus paradisi* Macfadyen) seedlings (40–50 cm tall) in an insect rearing room at $25 \pm 1^\circ\text{C}$, $80 \pm 5\%$ RH and a photoperiod of LD 14:10 h. A laboratory colony of *Coelophora inaequalis* was initiated with pupae collected from citrus trees on the campus of Fort Lauderdale Research and Education Center (FLREC), University of Florida, Broward County, Florida. The pupae were maintained in glass Petri dishes (15 cm diameter by 2.5 cm high) at 25°C for emergence. Newly emerged adults were paired and introduced into a screen cage (40 × 40 cm) and fed with brown citrus aphids on grapefruit seedlings. The aphids and host plants were replaced every 3–5 days. The cage was kept in the same insect rearing room as mentioned above. After a 4 month rearing period, the ensuing colonies were used for the tests. The identity of *T. citricida* was confirmed by its morphological characteristics as described by Halbert & Brown (1996), and *C. inaequalis* was confirmed by M. C. Thomas at the Division of Plant Industry (DPI), Florida Department of Agriculture and Consumer Services (FDACS), Gainesville, Florida. Voucher specimens were deposited at the collection of the DPI, FDACS.

Development of *C. inaequalis*

Studies on development of *C. inaequalis* were conducted at 20 and 25°C . For each experiment, ≈ 30 mated female *C. inaequalis* adults were held in glass containers (10 cm diameter × 8 cm high) along with fresh grapefruit leaves and sufficient brown citrus aphids for oviposition. Seventy and 74 freshly laid eggs were kept in glass Petri dishes at 20 and 25°C , respectively. They were observed daily for hatching. At each temperature, 45 newly hatched larvae were individually kept in glass vials (2.5 cm diameter × 10 cm high) supplied with aphids of mixed ages. Moulting was monitored twice daily. Brown citrus aphids were added and grapefruit leaves were replaced daily. We estimated the following life cycle parameters: development times of egg, each larval and combined larval stages, prepupal and pupal stages, as well as combined immature period (the time from egg to emerged adult). All developmental parameters were compared between two temperatures using the general linear model (GLM) procedure of SAS (SAS Institute Inc., Cary, NC, U.S.A., 1988). The Student's *t*-test was used to compare the survival rates between two temperatures. Percentage data were arcsine square-root transformed before analysis.

Functional response

Coelophora inaequalis pupae were collected from the laboratory colonies. Upon eclosion, female *C. inaequalis* adults were selected at random and isolated without food for 24 h before the trials. The predation arena consisted of a grapefruit leaf disk placed in a 100 mm by 15 mm Petri dish lined with wet filter paper. Prey densities of 4, 8, 16, 32 and 64 newly-moulted brown citrus aphid adults were placed on each leaf disk along with a single isolated *C. inaequalis* female. One replication of each density was conducted to determine the natural mortality of brown citrus aphids under the same conditions in the absence of predators. Each density was replicated 15 times and individual lady beetles were exposed to the aphids for 24 h and the number of prey consumed during each feeding period was recorded. All predation trials were conducted in growth chambers (Percival, Boone, Indiana, U.S.A.) at $25 \pm 1^\circ\text{C}$ and LD 14:10 h. Predation of brown citrus aphid by fourth-instar *C. inaequalis* larvae was examined as well. The test larvae were derived from laboratory colonies maintained for three generations, as described above. Experimental procedures for examining *C. inaequalis* larvae were the same as for adults.

The analysis of functional response was described by Juliano (1993). The shape of the functional response was determined by performing a logistic regression of the proportion of aphids consumed as a function of initial density using individual data points. A nonlinear least-squares regression (again using individual data points) was performed to estimate and compare parameters of the functional response for *C. inaequalis* larvae and adults using the 'random-predator' equation (Rogers, 1972):

$$N_e = N_0(1 - \exp[a(T_h N_e - T)])$$

where N_e = the number of aphids consumed, N_0 = the initial aphid density, a = the attack constant (or instantaneous search rate), T_h = prey handling time, and T = the total time available. A SAS program developed by Juliano (1993) using CATMOD and NLIN procedures (SAS Institute, 1988) was used to determine the shape of functional response and to fit the models. A two-way ANOVA was also used to test the effects of prey density and predator life stage on the numbers of prey consumed.

Results

Development of *C. inaequalis*

Developmental time and survivorship for the immature stages of *C. inaequalis* at 20 and 25°C are presented in Table 1. Egg developmental time was significantly shorter at 25°C (3.2 days) than at 20°C (5.2 days) ($F = 236.09$; d.f. = 1123; $P < 0.001$) and egg survivorship was also significantly higher at 25°C (89.2%) than at 20°C (84.3%) ($t = 9.81$; d.f. = 4; $P < 0.001$).

The developmental time of larvae was significantly longer at 20°C (11.7 days) than at 25°C (8.2 days) ($F = 102.01$; d.f. = 1, 65; $P < 0.001$). The survival rate of larvae was significantly lower at 20°C (49.2%) than at 25°C (57.6%) ($t = 10.29$; d.f. = 4; $P < 0.001$). The fourth-instar stage required more time than the preceding three stadia at both 20 and 25°C (Table 1).

Table 1 Developmental periods (days \pm SE) of immature stages of *C. inaequalis* feeding on *T. citricida* at 20 and 25 °C. The first value in parentheses is the number of beetles survived to next stage, and the second is the percentage of survival to the next stage. The initial number of eggs was 70 and 74 at 20 and 25 °C, respectively. ANOVA showed that means in each row were all different significantly at $P < 0.05$ (GLM, LSD).

Temp, °C	Egg	1st instar	2nd instar	3rd instar	4th instar	Total larval stage	Prepupa	Pupa	From egg to adult
20	5.2 \pm 0.11 (59, 84.3)	2.5 \pm 0.10 (47, 79.7)	2.2 \pm 0.12 (35, 74.5)	2.6 \pm 0.15 (32, 91.4)	4.1 \pm 0.18 (29, 90.6)	11.7 \pm 0.32 (29, 49.2)	1.8 \pm 0.08 (26, 89.7)	6.3 \pm 0.17 (24, 92.3)	24.7 \pm 0.48 (24, 34.3)
25	3.2 \pm 0.07 (66, 89.2)	1.5 \pm 0.07 (55, 83.3)	1.3 \pm 0.08 (45, 81.8)	1.9 \pm 0.10 (41, 91.1)	3.4 \pm 0.12 (38, 92.7)	8.2 \pm 0.18 (38, 57.6)	1.3 \pm 0.08 (31, 81.2)	3.2 \pm 0.15 (29, 93.5)	15.9 \pm 0.28 (29, 39.2)

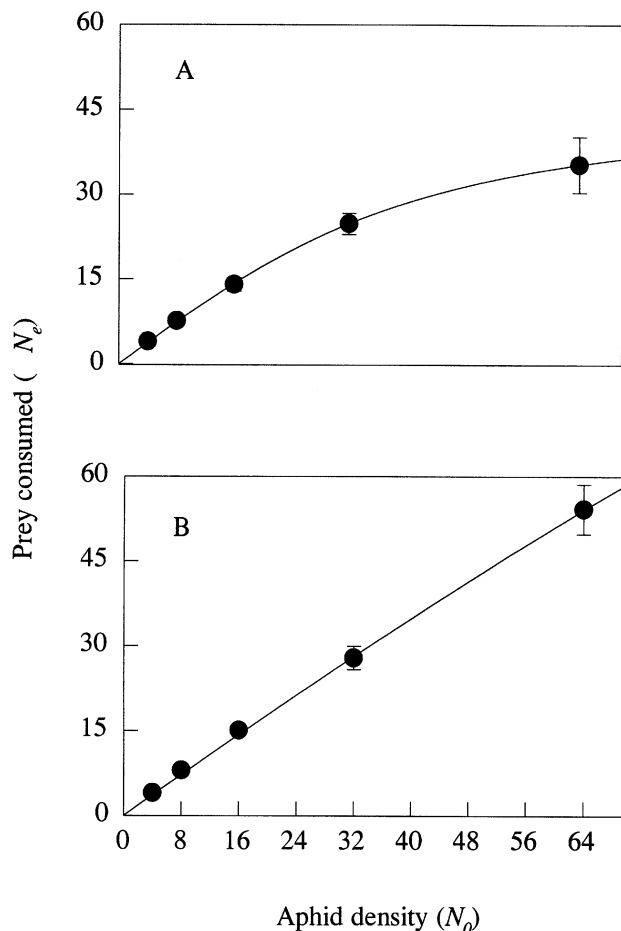


Figure 1 Functional responses of *C. inaequalis* larvae (A) and adult (B) feeding on *T. citricida*. Dots are mean observed value \pm 95% CL of 15 replicates. Curves are lines of best fit as predicted by type II functional responses. The estimates of parameter are: larvae, $a = 0.1305 \pm 0.0257$, $T_h = 30.41$ (95% CI, 2.7947); adult, $a = 0.0989 \pm 0.0194$, $T_h = 5.75$ (95% CI, 4.5301). All coefficients are significantly different from 0 at $P < 0.05$.

Significant differences also were found for prepupae ($F = 16.21$; d.f. = 1, 55; $P < 0.001$) and pupal periods ($F = 179.30$; d.f. = 1, 51; $P < 0.001$). The survival rate of the prepupal stage was significantly higher at 20 °C (89.7%) than 25 °C (81.2%) ($t = 6.39$; d.f. = 4; $P = 0.003$), while survivorship of the pupal stage was not different significantly between 25 °C (93.5%) and 20 °C (92.3%) ($t = 1.89$; d.f. = 4; $P = 0.132$).

The combined developmental time from egg to adult of *C. inaequalis* averaged 24.7 days at 20 °C and declined significantly to 15.9 days at 25 °C ($F = 274.21$; d.f. = 1, 51; $P < 0.001$) and the survivorship for combined immature stages was significantly lower at 20 °C (34.3%) than at 25 °C (39.2%) ($t = 4.27$; d.f. = 4; $P = 0.013$; Table 1).

Functional response

Coelophora inaequalis adults consumed more aphids within a 24-h period than did fourth-instar larvae at any prey densities (Fig. 1). The two-way ANOVA results indicated that the number of aphids consumed was also significantly affected by *C. inaequalis* life stage ($F = 45.70$; d.f. = 1, 140; $P < 0.001$), initial aphid density ($F = 469.63$; d.f. = 4, 140; $P < 0.001$), and interaction between predator life stage and initial prey density ($F = 28.32$; d.f. = 4, 140; $P < 0.001$).

The proportion of aphids consumed by *C. inaequalis* fourth-instar larvae and adults declined monotonically with initial aphid density, indicating a type II functional response for both predator stages. This was further confirmed by logistic regression. The estimates of the linear coefficients were negative (i.e. the proportion of aphids consumed declined even at lower aphid densities) for *C. inaequalis* larvae (estimates = -0.1032 ± 0.0220 ; $\chi^2 = 22.04$, $P < 0.001$) and adults (estimates = -0.1805 ± 0.0343 ; $\chi^2 = 27.72$, $P < 0.001$), whereas the estimates of the quadratic coefficient was positive for *C. inaequalis* larvae (estimates = 0.0008 ± 0.0003 ; $\chi^2 = 8.98$, $P = 0.001$) and adults (estimates = 0.0019 ± 0.0004 ; $\chi^2 = 24.52$, $P < 0.001$).

The estimate of T_h was significantly larger for *C. inaequalis* larvae than for adults ($t = 4.63$; $t_{146} = 1.65$; $P < 0.05$). Based on the estimation, the fourth-instar larvae took seven times longer to search and consume brown citrus aphids than the adults. The estimate of a was larger for larvae as well. However, the difference was not significant ($t = 0.0316$; $t_{146} = 1.28$; $P > 0.10$). The fitted functions (Fig. 1A,B) for *T. citricida* as prey showed that the number of prey consumed by *C. inaequalis* adults increased more rapidly with increasing number of prey than the number consumed by fourth-instar larvae.

Discussion

Measuring the bionomics of a predator feeding on the target prey is one important step in assessing the potential of a biological control agent (Lucas *et al.*, 1997). The relationship between the

number of prey consumed and the available prey densities determines the type of functional response, which can in turn affect the dynamics of predator and prey populations and the stability of predator–prey systems (Hassell, 1978). Knowledge of prey items and rates of predation is especially critical in evaluating the potential effectiveness of a predator as a biological control agent. In addition, functional response curves can be used to infer basic mechanisms underlying predator–prey interactions, clarify coevolutionary relationships, and enhance biological control (Houck & Strauss, 1985). Based on our observations, *C. inaequalis* is one of the most abundant coccinellid predators of *T. citricida* occurring in the citrus groves in South Florida (unpublished data). Similar observations also were reported by Michaud (1998) in Puerto Rico. However, the most abundant coccinellids on *T. citricida* was *C. sanguinea* in the Dominican Republic (Borbon *et al.*, 1992), Cuba (Batista *et al.*, 1995), Venezuela (Morales & Burandt, 1985) and Brazil (Lara *et al.*, 1977; Bartoszeck, 1980). The results of the current study demonstrated that *C. inaequalis* could complete its life cycle feeding on *T. citricida* with relatively high survival rate at 20 and 25 °C, indicating that *T. citricida* is a suitable prey for *C. inaequalis*. This is consistent with the report of Michaud (1998) that *C. inaequalis* and *Cycloneda sanguinea* L. collected in Puerto Rico developed normally and had good survival rates on *T. citricida*. However, Tao & Chiu (1971) reported that 5 of 13 coccinellid species fed on *T. citricida* suffered injury or death. Parker & Singh (1973) found that the coccinellids *Chilocorus politus* Muls., *Coccinella arcuata* F. and *Micraspis (Slesia) discolor* (F.) all expressed a non-preference for *T. citricida* in feeding trials. More recently, Morales & Burandt (1985) reported that *C. sanguinea* immatures collected in Venezuela failed to develop into adults when fed either live or dry *T. citricida*. The differences could be attributable to the differences between biotypes of predator with respect to their ability to utilize *T. citricida* as food (Michaud, 1998).

Numerous mechanistic and phenomenological models have been used to describe functional responses. Although many different models may be employed, the issues involved in statistical analyses of functional responses are similar (Juliano, 1993). Many investigators have analysed experiments without replacement of prey, but employed the models appropriate for predation with constant prey density (Livdahl, 1979; Juliano & Williams, 1985). Juliano (1993) stated that the ‘random-predator’ model is the appropriate model to use for such analysis, rather than the typical Holling Disk equation (Holling, 1959, 1966), because prey were depleted during the experiment. Our results showed that consumption of *T. citricida* by both *C. inaequalis* adults and fourth-instar larvae demonstrated a type II functional response (Fig. 1A,B). This is consistent with the report by Morales & Burandt (1985) that *C. sanguinea* feeding on *T. citricida* also corresponded to Holling’s type II functional response. Based on parameter estimates (Fig. 1A, B), *C. inaequalis* adults showed shorter handling time and lower search rate compared to larvae. *Coelophora inaequalis* larvae took longer to process *T. citricida*, but are more efficient at locating their prey, requiring fewer aphids to reach saturation than adults. Wells & McPherson (1999) reported similar findings with *Hippodamia convergens* Guerin-Meneville adults consuming significantly greater numbers of tobacco aphids, *Myzus*

nicotianae Blackman, than did fourth-instar larvae. They concluded that the increased consumption by adults relative to larvae might be caused by digestion or handling time differences.

The present study has provided us with a better understanding of the predator–prey relationship between *C. inaequalis* and *T. citricida*. Although our results suggest that *C. inaequalis* appears to be an efficient predator of *T. citricida* in South Florida, more realistic field experiments are needed to assess the impact of *C. inaequalis* on *T. citricida* in citrus groves.

Acknowledgements

J.-J. Wang is a postdoctoral research associate from Department of Plant Protection, South-west Agricultural University, Chongqing, The Peoples’ Republic of China. We are grateful to Dr Kimberly A. Klock-Moore for reviewing the manuscript. Florida Agricultural Experiment Station Journal Series No. R.-07829.

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Accepted 5 December 2000