



Effect of Temperature on Functional Response of *Aphidius gifuensis* (Hymenoptera: Braconidae) Parasitizing *Myzus persicae* (Hemiptera: Aphididae)

Authors: Khan, Muhammad Akbar Zafar, Liang, Qifu, Maria, Munoz San Martin, and Liu, Tong-Xian

Source: Florida Entomologist, 99(4) : 696-702

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.099.0419>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Effect of temperature on functional response of *Aphidius gifuensis* (Hymenoptera: Braconidae) parasitizing *Myzus persicae* (Hemiptera: Aphididae)

Muhammad Akbar Zafar Khan, Qifu Liang, Munoz San Martin Maria, and Tong-Xian Liu*

Abstract

Aphidius gifuensis Ashmead (Hymenoptera: Braconidae) is a common parasitoid of aphids including the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). To maximize the use of *A. gifuensis* for biological control of *M. persicae*, the functional response of *A. gifuensis* using *M. persicae* as a host was determined at 4 constant temperatures (15, 20, 25, and 30 °C) and 20 host densities (5, 10, 15, increased incrementally by 5, to a maximum of 100) on a 6-leaf sweet pepper plant (30 cm in height) over a 24 h period. Roger's random parasitoid equation (RRPE) and Holling's disc equation (HDE) were used to fit the data. The results showed that functional responses at all temperatures were type II, and the instantaneous attack rate (a) in both models increased as temperature increased from 15 to 25 °C and then decreased at 30 °C. The highest instantaneous attack rate (a) for *A. gifuensis* was at 25 °C for the 2 models, $1.3203 \pm 0.0415 \text{ d}^{-1}$ for HDE and $4.295 \times 10^3 \text{ d}^{-1}$ for RRPE. The handling time (T_h) for *A. gifuensis* by HDE was between $0.0105 \pm 0.0002 \text{ d}$ at 20 °C and $0.0214 \pm 0.0009 \text{ d}$ at 30 °C and by RRPE was between $1.265 \times 10^{-2} \pm 3.808 \times 10^{-4} \text{ d}$ at 20 °C and $0.0218 \pm 0.0010 \text{ d}$ at 30 °C. *Aphidius gifuensis* achieved its highest parasitism rate at medium temperatures. The results from this study showed that *A. gifuensis* performed best at 20 °C, suggesting that this parasitoid will be more effective as a biological control agent for *M. persicae* when the temperature is under 30 °C.

Key Words: biological control; Holling's disc model; Roger's random parasitoid model; sweet pepper; China

Resumen

Aphidius gifuensis Ashmead (Hymenoptera: Braconidae) es uno de los parásitos comunes de áfidos, entre los que se incluye el áfido verde del melocotón, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). Para potenciar el uso de *A. gifuensis* como control biológico de *M. persicae*, se determinó la respuesta funcional de *A. gifuensis* utilizando *M. persicae* como hospedador a cuatro temperaturas constantes (15, 20, 25 y 30 °C) y 20 densidades de hospedador (5, 10, 15, aumentó gradualmente por 5, a un máximo de 100) en una planta de pimiento dulce de 6 hojas (30 cm de altura) durante un periodo de 24 horas. Se utilizaron el modelo de parásito aleatorio de Roger y el modelo de disco de Holling para ajustar los datos. Los resultados mostraron que las respuestas funcionales en todas las temperaturas fueron de tipo II y los resultados mostraron que la tasa de ataque instantáneo (a) en ambos modelos incrementó a medida que la temperatura incrementaba desde 15 a 25 °C y después disminuyó a 30 °C. La tasa más alta de ataque instantáneo para *A. gifuensis* se obtuvo a 25 °C en ambos modelos, $1.3203 \pm 0.0415 \text{ día}^{-1}$ por el modelo de disco de Holling y $4.295 \times 10^3 \text{ día}^{-1}$ por el modelo de Roger. El tiempo de manipulación (T_h) para *A. gifuensis* por el modelo de Holling fue entre $0.0105 \pm 0.0002 \text{ día}$ a 20 °C y $0.0214 \pm 0.0009 \text{ día}$ a 30 °C y por el modelo de Roger fue entre $1.265 \times 10^{-2} \pm 3.808 \times 10^{-4} \text{ día}$ a 20 °C y $0.0218 \pm 0.0010 \text{ día}$ a 30 °C. *Aphidius gifuensis* logró la tasa de parasitismo más alta a temperaturas medias. Los resultados de este estudio mostraron que *A. gifuensis* actuó mejor a 20 °C, lo que sugiere que este parásito puede ser más efectivo como control biológico de *M. persicae* cuando la temperatura es inferior a 30 °C.

Palabras Clave: control biológico; modelo de disco de Holling; parasitoides modelo al azar de Roger; pimienta dulce; China

Insect parasitoids are very important in population and behavioral studies because they are abundant in nature and are significant biological control agents of many pests (Godfray 1994). The objective of ecological studies on parasitoids is to find the properties that are essential for the parasitoid to be a good biocontrol agent. Among these properties is their functional response (Berryman 1999). The functional response describes the number of hosts attacked by an individual natural enemy in relation to host density over a given time period (Solomon 1949). The number of hosts attacked increases as host densities increase, and there is an upper limit to the number of hosts attacked, due to satiation in the case of predators (Mills 1982), and due to limita-

tion of eggs or handling time problems in the case of parasitoids (Getz & Mills 1996). The type of functional response depends upon the response curve's shape below the upper limit. Response curves show the parasitoid–host interaction and are helpful in forecasting suitability of parasitoids in biological control programs.

Generally, the functional response is the intake rate by the consumer as a function of food density. There are 3 types, known as Holling's type I, II, and III. The type I response shows a linear increase, the type II response shows a hyperbolic increase, and the type III response shows a sigmoidal increase in the number of hosts attacked (Holling 1959). The parasitoid–host population is altered by each type of functional response. In the type

State Key Laboratory of Crop Stress Biology for Arid Areas, Northwest A&F University, Yangling, Shaanxi 712100, China; and Key Laboratory of Northwest Loess Plateau Crop Pest Management of Ministry of Agriculture, Northwest A&F University, Yangling, Shaanxi 712100, China; E-mail: akbarzafarkhan@yahoo.com (M. A. Z. K.), k861225@163.com (Q. L.), mariamunozsm@gmail.com (M. S. M. M.), txliu@nwsuaf.edu.cn (T.-X. L.)

*Corresponding author; E-mail: txliu@nwsuaf.edu.cn (T.-X. L.)

I functional response, there is density-independent parasitism; in type II, there is inverse density-dependent parasitism; and in type III, there is a direct density-dependent interaction at low host density that leads to the stabilization of parasitoid–host interaction. As the host density increases, the response also increases and then levels off (Hassell 2000). Stability is a very important aspect of biological control programs.

Aphidius gifuensis Ashmead (Hymenoptera: Braconidae) is a very important parasitoid of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) in Japan (Takada 2002) and China (Pan & Liu 2014). *Aphidius* species are well-known parasitoids and are extensively used in biological control programs of aphids (Starý et al. 1988). The genus *Aphidius* comprises many species including *Aphidius colemani* Viereck, *Aphidius ervi* Haliday, and *Aphidius matricariae* Haliday. These species are commercially available and are mostly used in greenhouses and fields against aphids (van Steenis & El-Khawass 1995; Grasswitz 1998). *Aphidius* are small wasps whose females lay eggs in aphid nymphs, and the larvae of the wasps consume the aphids from inside. As the larvae mature and the aphids are killed, the aphids turn into mummies, and after pupation adult wasps emerge from the mummies (Hagvar & Hofsvang 1991). Evaluation of the parasitism potential of these parasitoids is very important in developing integrated pest management programs for aphid control.

The green peach aphid, *M. persicae*, is a common pest of vegetable crops belonging to the families Solanaceae and Brassicaceae. The distribution of *M. persicae* is throughout the southern to the northern temperate zones. *Myzus persicae* has more than 875 secondary host plant species which include vegetables, crops, and ornamental plants (Ro et al. 1998). Aphids damage plants in many ways; by direct feeding, by releasing honeydew, or by transmitting viruses, for example, Cucumber mosaic virus, Pepper vein mottle virus, and Sweet potato leaf curl virus (Schepers 1988). Chemical control has commonly been used against aphids in greenhouses (Parrella et al. 1999), but at present there is an increase in insecticide resistance and cross-resistance in *M. persicae*, and insecticides also cause environmental pollution (Lee & Kang 2004). To reduce insecticide use, natural enemies of aphids are being used for biological control to protect greenhouse crops. In greenhouse crops, the objective is to suppress the pest population in the latent phase of pest development rather than to reduce an already dense pest population. The early introduction of a natural enemy in order to decrease latent phase growth is aimed to cause mortality associated with a functional response (Wiedenmann & Smith 1997).

In many previous studies scientists have used Petri dishes for functional response experiments, but in this study we used sweet pepper plants (6-leaf stage) in plastic pots for functional response experiments. The objective of this study was to determine the effect of temperatures on the functional response curve. We tested 2 functional response curves to determine which model fits best. These models will provide information that can be used in developing better pest management programs against aphids in greenhouses and fields.

Materials and Methods

Experimental work was done in the Key Laboratory of Applied Entomology, Northwest A&F University, Yangling (34.2833°N, 108.0617°E), Shaanxi, China. The experiments were started on 1 Jan 2014 and ended on 30 Dec 2015.

HOST PLANT

Sweet pepper seeds, *Capsicum annuum* L. ‘Qiemen-Tianjiao’ (Solanaceae), were grown in plastic pots (15 × 15 cm) a mixture of ver-

miculite, peat moss, and perlite “Pindstrup Substrate” (Pindstrup Horticulture Ltd., Shanghai, China) at a 4:1:1 ratio by volume. The sweet pepper plants in plastic pots were placed in growth chambers. One plant was grown per plastic pot. Plants were germinated in growth chambers maintained at 25 ± 1 °C, 75 ± 5% RH, with a light intensity of 1,400 to 1,725 lx and a photoperiod of 16:8 h L:D. After germination, sweet pepper plants were transferred to air-conditioned insectaries at 25 ± 1 °C, 65 ± 5% RH, with a light intensity of 1,400 to 1,725 lx and a photoperiod of 16:8 h L:D. Sweet pepper plants at the 6-leaf stage were used for functional response experiments. Dry soluble fertilizer “Harvest More 20-20-20+TE” (Stoller Enterprises, Inc, Houston, Texas) at a rate of 1 g/L of water was applied to plants at 7 d intervals.

INSECT CULTURE

Myzus persicae living aphids and mummies were collected from sweet pepper in greenhouses at Yangling City, Shaanxi Province, China, in Jun 2013. Aphids were reared on sweet pepper plants in large net cages (60 × 60 × 60 cm) in air-conditioned insectaries at 25 ± 2 °C, 65 ± 5% RH, with light intensity of 1,400 to 1,725 lx and a photoperiod of 16:8 h L:D. After emergence from mummies, the parasitoids were reared on sweet pepper plants infested with *M. persicae*. The populations of aphids and parasitoids were maintained in air-conditioned insectaries for many generations and then used in functional response experiments.

FUNCTIONAL RESPONSE STUDY

There were 4 temperatures (15, 20, 25, and 30 °C), 20 aphid densities (from 5 to 100 per plant, at increments of 5), and 4 replications of all treatments. Individual pots, containing 1 sweet pepper plant at the 6-leaf stage were covered by a plastic cage (30 × 15 cm). The top of the cage was covered by a nylon net for air transfer. A small Petri dish (3.5 × 1 cm) with 10% honey water solution was placed inside the plastic cage for the parasitoids. These cages were placed in growth chambers. *Myzus persicae* 3rd instars were used in this study. After emergence from mummies, *A. gifuensis* wasps were sexed, and 1 male and 1 female were allowed to mate in small vials; 1 to 2 d later, 1 mated female was released in each plastic cage for each aphid density for 24 h and then removed. Aphids were observed daily for the presence of brownish mummies.

DATA ANALYSES

A 2-step approach was used to analyze the experimental data for functional responses. Data were first checked to see whether they showed a type II or type III functional response. A cubic logistic regression (Equation 1) between the proportion of aphids parasitized and the number of aphids was performed to find the shape of the curve (Juliano 2001).

$$\frac{N_{par}}{N} = \frac{\exp(P_0 + P_1N + P_2N^2 + P_3N^3)}{1 + \exp(P_0 + P_1N + P_2N^2 + P_3N^3)} \quad (1)$$

N_{par} is the number of aphids parasitized, N is the number of aphids offered, and P_0 , P_1 , P_2 and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively. If the linear coefficient (P_1) is significantly negative, the response is type II, and if it is significantly positive, the response is type III (Juliano 2001). HDE and RRPE were used to calculate the handling times and attack coefficients of a type II functional response. Equation 2 expresses HDE (Holling 1959), and Equation 3 expresses RRPE (Rogers 1972).

$$N_{par} = \frac{aTN}{1 + aT_h N} \quad (2)$$

$$N_{par} = N \left[1 - \exp\left(-\frac{aT}{1 + aT_h N}\right) \right] \quad (3)$$

N_{par} is the number of aphids parasitized, N is the number of aphids offered, a is attack rate, T_h is handling time, and T is the total time offered for parasitoid. R version 2.15.0 (R Development Core Team 2012) statistical software was used for parameter estimation in all above equations. If R statistical software was unable to give results, we used Solver tool in Microsoft Excel 2010 for parameter estimation in nonlinear regression.

Results

Logistic regressions for *A. gifuensis* at all 4 temperatures showed significant linear parameters $P_1 < 0$ (Table 1). The number of aphids parasitized by *A. gifuensis* hyperbolically approached the asymptote as aphid numbers increased, estimated both by HDE (Fig. 1) and by RRPE (Fig. 2). Thus, according to both models, *A. gifuensis* at all 4 temperatures showed type II functional responses. Attack rates (a) and handling times (T_h) of *A. gifuensis* were estimated by both HDE (Table 2) and RRPE (Table 3) at 4 temperatures. Equations 4, 5, 6, and 7 show the logistic regression analysis with estimated values of parameters at 15, 20, 25, and 30 °C, respectively.

$$\frac{N_{par}}{N} = \frac{\exp[4.759e + 00] + (-1.667e - 01)N + (2.143e - 03)N^2 + (-9.754e - 06)N^3}{1 + \exp[4.759e + 00] + (-1.667e - 01)N + (2.143e - 03)N^2 + (-9.754e - 06)N^3} \quad (4)$$

$$\frac{N_{par}}{N} = \frac{\exp[1.099e + 01] + (-3.782e - 01)N + (4.667e - 03)N^2 + (-1.968e - 05)N^3}{1 + \exp[1.099e + 01] + (-3.782e - 01)N + (4.667e - 03)N^2 + (-1.968e - 05)N^3} \quad (5)$$

$$\frac{N_{par}}{N} = \frac{\exp[5.244e + 00] + (-1.403e - 01)N + (1.428e - 03)N^2 + (-5.524e - 06)N^3}{1 + \exp[5.244e + 00] + (-1.403e - 01)N + (1.428e - 03)N^2 + (-5.524e - 06)N^3} \quad (6)$$

$$\frac{N_{par}}{N} = \frac{\exp[2.176e + 00] + (-1.001e - 01)N + (1.263e - 03)N^2 + (-5.664e - 06)N^3}{1 + \exp[2.176e + 00] + (-1.001e - 01)N + (1.263e - 03)N^2 + (-5.664e - 06)N^3} \quad (7)$$

Attack rates (a) of *A. gifuensis* modeled by HDE are presented in Table 2. At 25 °C, the attack rate was $1.3203 \pm 0.0415 \text{ d}^{-1}$ and was significantly greater than at the others temperatures. At 20 °C, the attack rate was $1.3142 \pm 0.0312 \text{ d}^{-1}$ and was significantly lower than at 25 °C. At 15 °C, the attack rate was $1.1323 \pm 0.0191 \text{ d}^{-1}$ and was significantly lower than at 20 °C. At 30 °C, the attack rate was $0.7999 \pm 0.0393 \text{ d}^{-1}$ and was significantly lower than at all other temperatures. Attack rates were highest at 20 and 25 °C, indicating that parasitism was greatest at these temperatures.

Handling times (T_h) of *A. gifuensis* modeled by HDE are also presented in Table 2. At 30 °C, the handling time was $0.0214 \pm 0.0009 \text{ d}$ and was significantly longer than at all other temperatures. At 15 and 25 °C, handling times were the same with $0.0120 \pm 0.0003 \text{ d}$ and were shorter than at 30 °C. At 20 °C, the handling time was $0.0105 \pm 0.0002 \text{ d}$ and was the shortest among all the temperatures, indicating that parasitism was best at 20 °C.

Thus, according to HDE, the attack rate was highest at 20 and 25 °C and the handling time shortest at 20 °C. Equations 8, 9, 10, and 11 show HDE with modeled values of attack rate (a) and handling time (T_h) at 15, 20, 25, and 30 °C, respectively.

$$N_{par} = \frac{(1.1323)TN}{1 + (1.1323)(0.0129)N} \quad (8)$$

$$N_{par} = \frac{(1.3142)TN}{1 + (1.3142)(0.0105)N} \quad (9)$$

$$N_{par} = \frac{(1.3203)TN}{1 + (1.3203)(0.0120)N} \quad (10)$$

$$N_{par} = \frac{(1.7999)TN}{1 + (1.7999)(0.0214)N} \quad (11)$$

Attack rates (a) and handling times (T_h) of *A. gifuensis* modeled by RRPE are presented in Table 3. For 25 °C, R statistical software was unable to estimate parameter values, wherefore the attack rate (a) and

Table 1. Results of logistic regression analysis, with estimates and standard errors (SE) of linear, quadratic, and cubic coefficients for the proportion of aphids parasitized by *Aphidius gifuensis* against increasing aphid densities offered at various constant temperatures.

Temperature	Coefficient	Estimate	SE	Z value	Pr(> Z)
15 °C	Constant (P_0)	4.759e+00	1.204e-01	39.51	<2e-16 ***
	Linear (P_1)	-1.667e-01	6.506e-03	-25.63	<2e-16 ***
	Quadratic (P_2)	2.143e-03	1.094e-04	19.59	<2e-16 ***
	Cubic (P_3)	-9.754e-06	5.753e-07	-16.96	<2e-16 ***
20 °C	Constant (P_0)	1.099e+01	2.981e-01	36.85	<2e-16 ***
	Linear (P_1)	-3.782e-01	1.398e-02	-27.05	<2e-16 ***
	Quadratic (P_2)	4.667e-03	2.099e-04	22.23	<2e-16 ***
	Cubic (P_3)	-1.968e-05	1.011e-06	-19.46	<2e-16 ***
25 °C	Constant (P_0)	5.244e+00	1.532e-01	34.22	<2e-16 ***
	Linear (P_1)	-1.403e-01	7.930e-03	-17.7	<2e-16 ***
	Quadratic (P_2)	1.428e-03	1.292e-04	11.06	<2e-16 ***
	Cubic (P_3)	-5.524e-06	6.631e-07	-8.33	<2e-16 ***
30 °C	Constant (P_0)	2.176e+00	7.392e-02	29.43	<2e-16 ***
	Linear (P_1)	-1.001e-01	4.474e-03	-22.37	<2e-16 ***
	Quadratic (P_2)	1.263e-03	8.172e-05	15.46	<2e-16 ***
	Cubic (P_3)	-5.664e-06	4.558e-07	-12.43	<2e-16 ***

Asterisks indicate significance level: ***, 0.001.

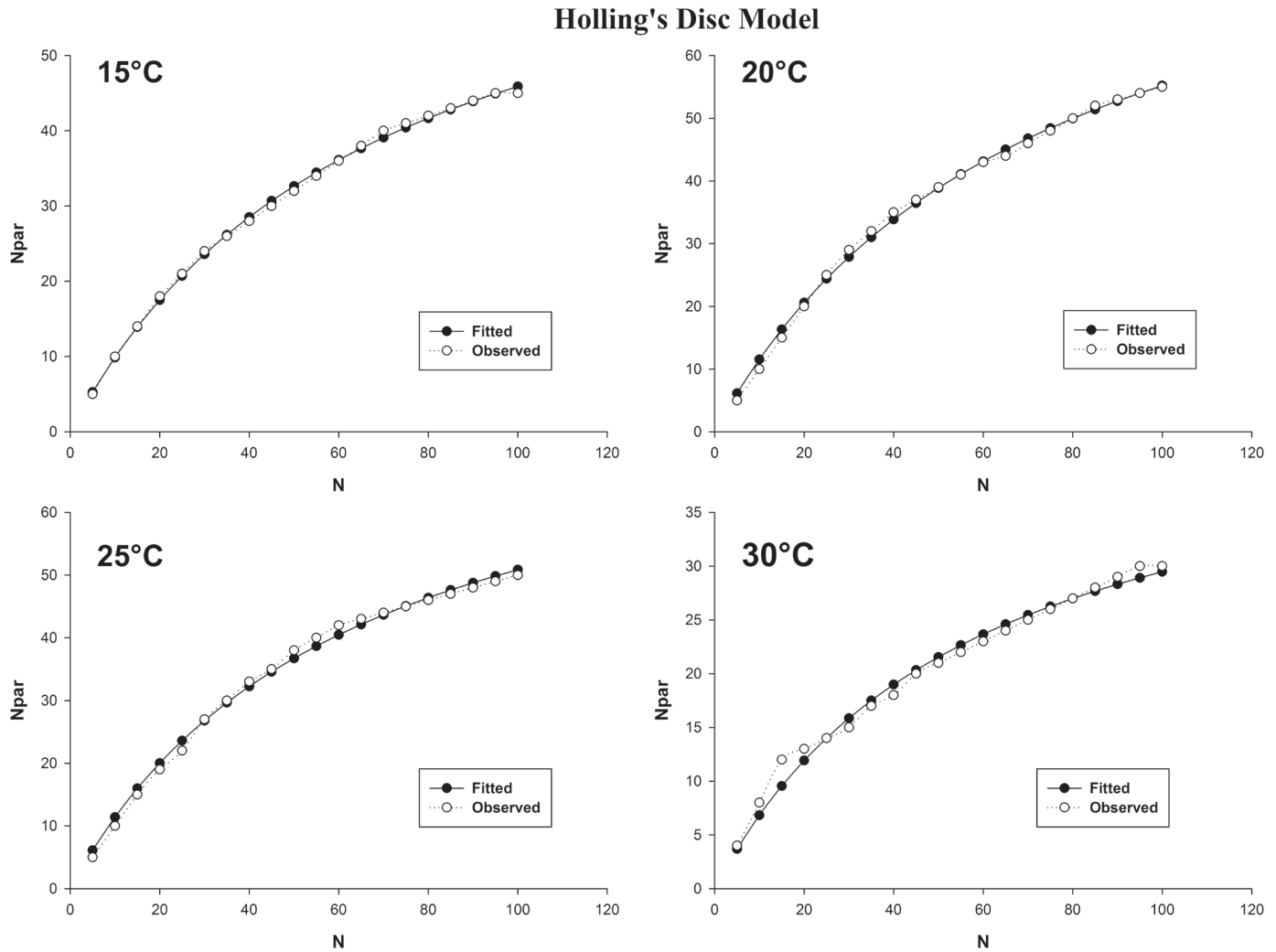


Fig. 1. Type II functional response curves fitted by Holling’s disc equation (HDE) of *Aphidius gifuensis* against *Myzus persicae* at various temperatures.

handling time (T_h) were estimated by Solver tool in Microsoft Excel 2010. This tool provides only the parameter values, so standard errors and other statistical values at 25 °C could not be listed in Table 3. At 25 °C, the attack rate was $4.295e+03 \text{ d}^{-1}$ and was highest among all temperatures. At 20 °C, the attack rate was $1.153e+02 \pm 3.655e+02 \text{ d}^{-1}$ and was lower than at 25 °C. At 15 °C, the attack rate was $4.3759 \pm 0.4184 \text{ d}^{-1}$ and was lower than at 20 °C. At 30 °C, the attack rate was $1.4721 \pm 0.1469 \text{ d}^{-1}$ and was the lowest among all temperatures. As found with the HDE model, these results also showed that attack rates were highest at 20 and 25 °C.

At 30 °C, the handling time was $0.0218 \pm 0.0010 \text{ d}$ and was the significantly longest among all the temperatures (Table 3). At 15 and 25 °C, handling times were the same with 0.0144 d and shorter than at 30 °C. At 20 °C, the handling time was $1.265e-02 \pm 3.808e-04 \text{ d}$ and was the shortest among all the temperatures. The handling time was longest at 30 °C and shortest at 20 °C. Equations 12, 13, 14, and 15 show RRPE with modeled values of attack rate (a) and handling time (T_h) at 15, 20, 25, and 30 °C, respectively.

$$N_{par} = N \left[1 - \exp\left(-\frac{(4.3759)T}{1 + (4.3759)(0.0141)N}\right) \right] \quad (12)$$

$$N_{par} = N \left[1 - \exp\left(-\frac{(1.153e + 02)T}{1 + (1.153e + 02)(1.265e - 02)N}\right) \right] \quad (13)$$

$$N_{par} = N \left[1 - \exp\left(-\frac{(4.295e + 03)T}{1 + (4.295e + 03)(0.0144)N}\right) \right] \quad (14)$$

$$N_{par} = N \left[1 - \exp\left(-\frac{(1.4721)T}{1 + (1.4721)(0.0218)N}\right) \right] \quad (15)$$

Discussion

This study of functional responses was a preliminary step in evaluating the efficiency of the parasitoid *A. gifuensis* in biological control programs (Overholt & Smith 1990). In our study, Petri dishes were not used as in many previous studies (van Steenis & El-Khawass 1995; Donnelly & Phillips 2001; Farrokhi et al. 2010). We believe that the use of sweet peppers planted in pots provides a better understanding of functional responses, because the environment is more open as compared with Petri dishes. Our results demonstrated that temperature had a significant effect on the functional response of *A. gifuensis* to *M. persicae*. At all 4 temperatures, linear parameters (P_i) were negative (Table 1), showing that the functional responses were type II. A type II functional response has been found by many scientists with other insect species under various conditions (Bernal et al. 1994; De Clercq

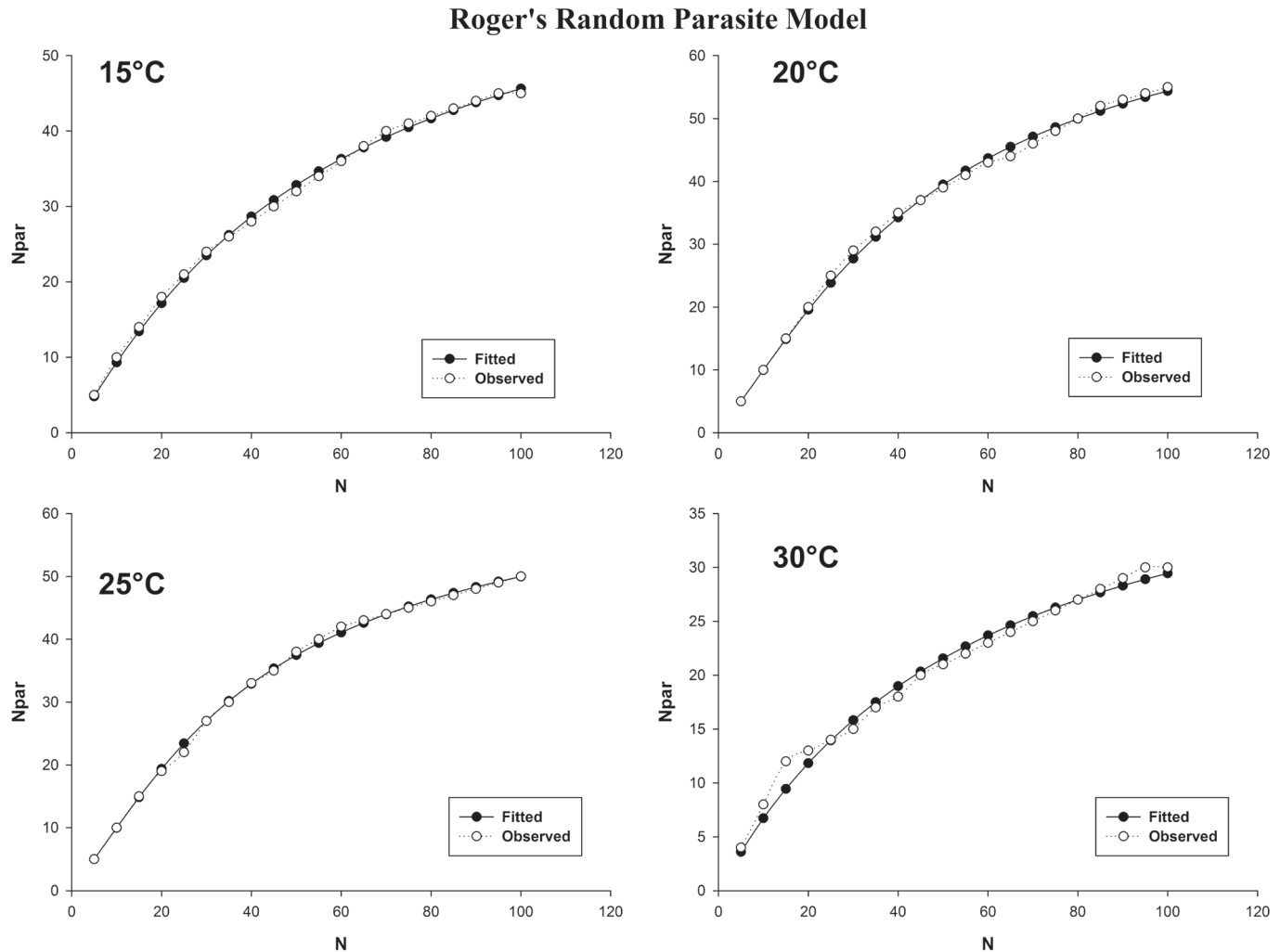


Fig. 2. Type II functional response curves fitted by Roger's random parasitoid equation (RRPE) of *Aphidius gifuensis* against *Myzus persicae* at various temperatures.

et al. 2000; Zamani et al. 2006; Fathi & Nouri-Ganbalani 2009). Holling (1959) stated that invertebrates display a type II functional response whereas type III is found in vertebrate predators, but later this idea was rejected because parasitoids can also display a type III functional response. Wang & Ferro (1998) found a type II functional response at low temperatures and a type III functional response at high temperatures in experiments with *Trichogramma ostrinae* Pang & Chen (Hymenoptera: Trichogrammatidae) parasitizing *Ostrinia nubilalis* Hübner

(Lepidoptera: Noctuidae). In the present study, at all temperatures *A. gifuensis* showed a type II functional response. Functional response types and estimated parameters for an insect species could be affected by many factors such as temperature, type of prey or host, and host plant (Juliano & Williams 1985; Coll & Ridgway 1995; Runjie et al. 1996; Messina & Hanks 1998; Moezipour et al. 2008).

Our results also indicated that there was a considerable difference between the values of parameters modeled by HDE and RRPE. Values

Table 2. Estimate and standard error (SE) of attack rate (a) and handling time (T_h) of *Aphidius gifuensis* on *Myzus persicae* by Holling's disc equation (HDE) at various constant temperatures.

Temperature	Coefficient	Estimate	S.E.	t value	$Pr(> t)$
15 °C	Attack rate (a) (d^{-1})	1.1323	0.0191	59.21	<2e-16***
	Handling time (T_h) (d)	0.0129	0.0002	57.17	<2e-16***
20 °C	Attack rate (a) (d^{-1})	1.3142	0.0312	42.02	<2e-16***
	Handling time (T_h) (d)	0.0105	0.0002	38.50	<2e-16***
25 °C	Attack rate (a) (d^{-1})	1.3203	0.0415	31.78	<2e-16***
	Handling time (T_h) (d)	0.0120	0.0003	32.96	<2e-16***
30 °C	Attack rate (a) (d^{-1})	0.7999	0.0393	20.32	7.32e-14***
	Handling time (T_h) (d)	0.0214	0.0009	22.39	1.37e-14***

Asterisks indicate significance level: ***, 0.001.

Table 3. Estimate and standard error (SE) of attack rate (a) and handling time (T_h) of *Aphidius gifuensis* on *Myzus persicae* by Roger's random parasitoid equation (RRPE) at various constant temperatures.

Temperature	Coefficient	Estimate	SE	t value	Pr(> t)
15 °C	Attack rate (a) (d^{-1})	4.3759	0.4184	10.46	4.47e-09
	Handling time (T_h) (d)	0.0141	0.0003	44.34	<2 -16***
20 °C	Attack rate (a) (d^{-1})	1.153e+02	3.655e+02	0.32	0.756
	Handling time (T_h) (d)	1.265e-02	3.808e-04	33.22	<2e-16***
25 °C	Attack rate (a) (d^{-1})	4.295e 03	N/A	N/A	N/A
	Handling time (T_h) (d)	0.0144	N/A	N/A	N/A
30 °C	Attack rate (a) (d^{-1})	1.4721	0.1469	10.02	8.71e-09
	Handling time (T_h) (d)	0.0218	0.0010	20.99	4.16e-14

Asterisks indicate significance level: ***, 0.001; N/A denotes not available.

of parameters modeled using RRPE were high, which might be due to the exponential function (exp) in RRPE. For analysis of functional response experiments, a good model is very important to understanding the results. In this study, we tested 2 models. We compared HDE, which assumes constant host density and host replacement, with RRPE, which does not assume host replacement (Collins et al. 1981; Enkegaard 1994). HDE was better at estimating parameters compared with RRPE because the values of parameters modeled by HDE were simple, easy, and logical. Mohaghegh et al. (2001) and Allahyari et al. (2004) also found that HDE was better at estimating parameters when compared with RRPE.

Parasitism of *A. gifuensis* was higher between 20 and 25 °C and lower at 15 and 30 °C, indicating that *A. gifuensis* performs best when the temperature ranges from 20 to 25 °C. These results were similar to the findings of Ohta & Miura (2001). In our study, the highest attack rate (a) modeled using HDE at 25 °C was $1.3203 \pm 0.0415 d^{-1}$ and modeled by RRPE was $4.295e+03 d^{-1}$. The difference in values might be due to the exponential function in RRPE. Gordon (1985) observed that predation rate of *Coleomegilla maculata* (De Geer) (Coleoptera: Coccinellidae) on *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) eggs increased as temperature increased from 10 to 30 °C. Mack & Smilowitz (1982a, b) observed that the predation rate of *C. maculata* on *M. persicae* increased with temperature increase, but in our study the attack rate (a) increased up to 25 °C and then decreased at 30 °C. At 30 °C, the attack rate (a) of *A. gifuensis* was very low. The lowest attack rate (a) modeled by HDE at 30 °C was $0.7999 \pm 0.0393 d^{-1}$ and by RRPE was $1.4721 \pm 0.1469 d^{-1}$, indicating that the performance of the parasitoid is adversely affected by high temperatures. Handling times (T_h) were the shortest at 20 °C and the longest at 30 °C modeled by HDE and RRPE, suggesting that at 20 °C the parasitoid performs well and at high temperatures it performs badly.

In conclusion, temperature had a significant impact on functional responses and attack rates of *A. gifuensis* on *M. persicae*. The results of this study may be useful for sweet pepper growers who want to use biological control against aphids in greenhouses. They will also be helpful for further research on *A. gifuensis* in integrated pest management programs against aphids in greenhouses and fields. The results of this functional response study can be used to predict the efficacy of this parasitoid in biological control programs, but additional data need to be collected in field situations (O'Neil, 1989).

Acknowledgments

Funding of this research was partially supported by each of the following grants: the National Natural Science Foundation of China (NO. 31272089), National Basic Research Program of China (973 Project No.

2013CB127600), and China Agriculture Research System (No.CARS-25-B-06). We also thank anonymous reviewers for giving valuable comments on the manuscript and all staff members of College of Plant Protection, Northwest Agriculture and Forestry University.

References Cited

- Allahyari H, Fard PA, Nozari J. 2004. Effects of host on functional response of offspring in two populations of *Trissolcus grandis* on the sunn pest. *Journal of Applied Entomology* 128: 39–43.
- Bernal JS, Bellows TS, González D. 1994. Functional response of *Diaeretiella rapae* (McIntosh) (Hym., Aphidiidae) to *Diuraphis noxia* (Mordwilko) (Hom., Aphididae) hosts. *Journal of Applied Entomology* 118: 300–309.
- Berryman AA. 1999. The theoretical foundations of biological control, pp. 3–21. In Hawkins BA, Cornell HV [eds.], *Theoretical Approaches to Biological Control*. Cambridge University Press, Cambridge, United Kingdom.
- Coll M, Ridgway RL. 1995. Functional and numerical responses of *Orius insidiosus* (Heteroptera: Anthracoridae) to its prey in different vegetable crops. *Annals of the Entomological Society of America* 88: 732–738.
- Collins M, Ward S, Dixon A. 1981. Handling time and the functional response of *Aphelinus thomsoni*, a predator and parasite of the aphid *Drepanosiphum platanoidis*. *Journal of Animal Ecology* 50: 479–487.
- De Clercq P, Mohaghegh J, Tirry L. 2000. Effect of host plant on the functional response of the predator *Podisus nigrispinus* (Heteroptera: Pentatomidae). *Biological Control* 18: 65–70.
- Donnelly BE, Phillips TW. 2001. Functional response of *Xylocoris flavipes* (Hemiptera: Anthracoridae)—effects of prey species and habitat. *Environmental Entomology* 30: 617–624.
- Enkegaard A. 1994. Temperature dependent functional response of *Encarsia formosa* parasitizing the Poinsettia-strain of the cotton whitefly *Bemisia tabaci* on Poinsettia. *Entomologia Experimentalis et Applicata* 73: 19–29.
- Farrokhi S, Ashouri A, Shirazi J, Allahyari H, Huigens ME. 2010. A comparative study on the functional response of *Wolbachia*-infected and uninfected forms of the parasitoid wasp *Trichogramma brassicae*. *Journal of Insect Science* 10: 1481–1489.
- Fathi SAA, Nouri-Ganbalani G. 2009. Assessing the potential for biological control of potato field pests in Ardabil, Iran: functional responses of *Orius niger* (Wolf.) and *O. minutus* (L.) (Hemiptera: Anthracoridae). *Journal of Pest Science* 83: 47–52.
- Getz WM, Mills NJ. 1996. Host–parasitoid coexistence and egg-limited encounter rates. *American Naturalist* 148: 333–347.
- Godfray HCJ [ed.]. 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.
- Gordon RD. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* 93: 1–912.
- Grasswitz TR. 1998. Effect of adult experience on the host-location behavior of the aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). *Biological Control* 12: 177–181.
- Hagvar EB, Hofsvang T. 1991. Aphid parasitoids (Hymenoptera: Aphidiidae): biology, host selection and use in biological control. *Biocontrol News and Information* 12: 13–41.
- Hassell MP [ed.]. 2000. *The spatial and temporal dynamics of host–parasitoid interactions*. Oxford University Press, London, United Kingdom.
- Holling CS. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91: 385–398.

- Juliano SA. 2001. Nonlinear curve fitting: predation and functional response curves, pp. 178–196 *In* Scheiner SM, Gurevitch J [eds.], *Design and Analysis of Ecological Experiments*. Oxford University Press, New York, New York.
- Juliano SA, Williams FM. 1985. On the evolution of handling time. *Evolution* 39: 212–215.
- Lee JH, Kang TJ. 2004. Functional response of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. *Biological Control* 31: 306–310.
- Mack TP, Smilowitz Z. 1982a. Using temperature-mediated functional response models to predict the impact of *Coleomegilla maculata* (DeGeer) adults and 3rd-instar larvae on green peach aphids. *Environmental Entomology* 11: 46–52.
- Mack TP, Smilowitz Z. 1982b. CMACSIM, a temperature-dependent predator–prey model simulating the impact of *Coleomegilla maculata* (DeGeer) on green peach aphids on potato plants. *Environmental Entomology* 11: 1193–1201.
- Messina FJ, Hanks JB. 1998. Host plant alters the shape of the functional response of an aphid predator (Coleoptera: Coccinellidae). *Environmental Entomology* 27: 1196–1202.
- Mills N. 1982. Satiation and the functional response: a test of a new model. *Ecological Entomology* 7: 305–315.
- Moezipour M, Kafil M, Allahyari H. 2008. Functional response of *Trichogramma brassicae* at different temperatures and relative humidities. *Bulletin of Insectology* 61: 245–250.
- Mohaghegh J, De Clercq P, Tirry L. 2001. Functional response of the predators *Podisus maculiventris* (Say) and *Podisus nigrispinus* (Dallas) (Hemiptera, Pentatomidae) to the beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera, Noctuidae): effect of temperature. *Journal of Applied Entomology* 125: 131–134.
- Ohta I, Miura KM. 2001. Life history parameters during immature stage of *Aphidius gifuensis* Ashmead (Hymenoptera: Braconidae) on green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Applied Entomology and Zoology* 36: 103–109.
- O'Neil RJ. 1989. Comparison of laboratory and field measurements of the functional response of *Podisus maculiventris* (Hemiptera: Pentatomidae). *Journal of the Kansas Entomological Society* 70: 40–48.
- Pan MZ, Liu TX. 2014. Suitability of three aphid species for *Aphidius gifuensis* (Hymenoptera: Braconidae): parasitoid performance varies with hosts of origin. *Biological Control* 69: 90–96.
- Parrella MP, Hansen LS, Van Lenteren JC. 1999. Glasshouse environments, pp. 819–839 *In* Fisher TW, Bellows TS, Caltagirone LE, Dahlstein DL, Huffaker CB, Gordh G [eds.], *Handbook of Biological Control*. Academic Press, San Diego, California.
- R Development Core Team. 2012. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ro TH, Long GE, Toba HH. 1998. Predicting phenology of green peach aphid (Homoptera: Aphididae) using degree-days. *Environmental Entomology* 27: 337–343.
- Rogers D. 1972. Random search and insect population models. *Journal of Animal Ecology* 41: 369–383.
- Runjie Z, Heong KL, Domingo IT. 1996. Relationship between temperature and functional response in *Cardiophiles philippinensis* (Hymenoptera: Braconidae), a larval parasitoid of *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae). *Environmental Entomology* 25: 1321–1324.
- Schepers A. 1988. Chemical control, pp. 89–121 *In* Minks AK, Harrewijn P [eds.], *Aphids: Their Biology, Natural Enemies and Control*, Volume 2C. Elsevier, New York, New York.
- Solomon M. 1949. The natural control of animal populations. *Journal of Animal Ecology* 18: 1–35.
- Starý P, Lyon JP, Leclant F. 1988. Biocontrol of aphids by the introduced *Lysiphlebus testaceipes* (Cress.) (Hymenoptera: Aphidiidae) in Mediterranean France. *Journal of Applied Entomology* 105: 74–87.
- van Steenis MJ, El-Khawass KAMH. 1995. Life history of *Aphis gossypii* on cucumber: influence of temperature, host plant and parasitism. *Entomologia Experimentalis et Applicata* 76: 121–131.
- Takada H. 2002. Parasitoids (Hymenoptera: Braconidae, Aphidiinae; Aphelinidae) of four principal pest aphids (Homoptera: Aphididae) on greenhouse vegetable crops in Japan. *Applied Entomology and Zoology* 37: 237–250.
- Wang B, Ferro DN. 1998. Functional responses of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) to *Ostrinia nubilalis* (Lepidoptera: Pyralidae) under laboratory and field conditions. *Environmental Entomology* 27: 752–758.
- Wiedenmann RN, Smith JW. 1997. Attributes of natural enemies in ephemeral crop habitats. *Biological Control* 10: 16–22.
- Zamani AA, Talebi AA, Fathipour Y, Baniamiri V. 2006. Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae) on the cotton aphid. *Journal of Pest Science* 79: 183–188.