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Functional response of *Trichogramma brassicae* at different temperatures and relative humidities

Mitra Moezipour[1], Maryam Kafil[2], Hossein Allahyari[2]
[1]*Department of Plant Protection, College of Agriculture, University of Technology, Isfahan, Iran*
[2]*Department of Plant Protection, College of Agriculture, University of Tehran, Karaj, Iran*

Abstract

Trichogrammatid egg parasitoids are the most promising biological control agents for inundative releases against Lepidopteran pests. *Trichogramma brassicae* Bezdenko is an egg parasitoid of the carob moth, *Apomyelois* (*Ectomyelois*) *ceratoniae* (Zeller), in Iranian Pomegranate orchards. Study on the functional response of natural enemies is one of the necessary features for the selection of natural enemies for biological control programs. In this study, laboratory tests were conducted to determine the functional response of *T. brassicae* on its factitious host, eggs of angoumois grain moth, *Sitotroga cerealella* (Olivier), at different temperatures and humidity. The type of functional response of *T. brassicae* was II at 25 °C and III at 20 and 30 °C (60% relative humidity). A model with indicator variable was used to compare the output parameters in different data sets. Analyses indicated that there is a significant difference in functional response of *T. brassicae* at 20 and 30 °C. Additional tests showed that changes at relative humidity can change the functional response parameters.

Key words: functional response, egg parasitoids, Trichogrammatidae, laboratory assessment, temperature, humidity.

Introduction

The carob moth, *Apomyelois* (*Ectomyelois*) *ceratoniae* (Zeller) (Lepidoptera Pyralidae), is the key pest of Pomegranate orchards in Iran that was first reported in Kashmar (Khorasan province), in 1972. It also produces significant damage on nut and fruit commodities such as almonds, Pistachios, Macadamias, as well as Pomegranates, stone and pomes fruits in many regions around the world (Botha *et al*., 2004). This pest continues its damage when the nuts stored under domestic storage conditions (Mehrnejad, 1995).

Egg parasitoids of the genus *Trichogramma* have been used successfully as inundative biological control agents against a range of agricultural pests mainly Lepidopterans and are the most widely used natural enemies in biological control world wide (Li *et al*., 1994). Augmentative release of mass-reared Trichogrammatid egg parasitoids have been identified as a promising method to reduce both egg hatching and subsequent damage due to larval feeding (Wajnberg and Hassan, 1994; Smith, 1996). Different native species of *Trichogramma* have been evaluated for controlling the carob moth in Iranian Pomegranate orchards (Moezipour, 2006). The most widespread species in Iran is *Trichogramma brassicae* Bezdenko (Hymenoptera Trichogrammatidae) (Azema and Mirabzadeh, 2005). The first studies were carried out on 1990 in Yazd province. Using *Trichogramma* wasps against this pest were also carried out during the years 1991-93, in Varamin (Tehran province). According to investigations egg parasitism was 37.4 and 57.84% in Khorasan and Yazd provinces, respectively. The most promising results were found in Yazd province (Moezipour, 2006).

The success of *Trichogramma* species depends on their efficiency in the field, maintenance and behaviour in laboratory, selection of adequate species and/or lineages besides thermal requirements, liberation techniques and evaluation of efficiency and dynamic models for parasitoids and hosts in the field (Parra *et al*., 1987). Climatic conditions plays an important role in tritrophic interactions among poikilotherms as it influences the level of control that natural enemies exert (Huffaker *et al*., 1971). Lack of quality control procedures during the mass production of natural enemies may lead to failures in biological control (van Lenteren *et al*., 2003). Correlation between values obtained at laboratory testing and field performance is important to be able to select a limited set of laboratory criteria that give meaningful information about performance after release (van Lenteren *et al*., 2003).

The functional response is an essential element of dynamics of host-parasitoid association and is an important determinant of the stability of the system (Oaten and Murdoch, 1975). Holling (1959; 1966) proposed three types of functional responses. In type I, number of killed host/prey rise as linear to a plateau; type II, a curvilinear rise to a plateau which then levels off under the influence of handling time or satiation and in type III predator/parasitoid response by a sigmoid increase in prey/hosts attacked (Hassell, 2000; Mills and Lacan, 2004). Functional response tests, shows the potential of parasitoid/predator ability to suppress the different density of prey/host.

An efficient artificial host must be able to produce high numbers of eggs and its eggs must be accepted by the parasitoid (Allahyari *et al*., 2004). *Sitotroga cerealella* (Olivier) (Lepidoptera Gelechiidae) is a suitable host for *T. brassicae* and used for mass rearing of *Trichogramma* wasps; so we used this host instead of target pest. In this study, we try to find the effect of different temperatures and humidity on the ability of *T. brassicae* in parasitizing the host eggs.

Materials and methods

Population of *Trichogramma* wasps were collected from Pomegranate in Yazd province. We collected individuals of Trichogrammatid populations from eggs of the carob moth in Pomegranate orchards in Yazd, Iran (35° 37" N, 50° 20" E). Based on morphometric analysis such as genitalia shape, collected wasps were identified as *T. brassicae*. Antennal characters were used to separate female and male Trichogramma individuals.

The *T. brassicae* colony was reared on eggs (<24 h old) of the factitious host, were obtained from a culture of *S. cerealella*, routinely reared in our laboratory. The Trichogrammatids were reared on factitious host, at 25 ± 1 °C, 55 ± 10% RH and 16: 8 (L: D) photoperiod.

Functional response experiments

The eight egg densities (4, 8, 10, 20, 40, 60, 80 and 120 eggs per adult parasitoid), were used. Glass shell vials (12×100 mm) served as experimental units. For each host density, eggs of factitious host (< 24 h) were placed on a small thick paper and inserted into glass vial. One-day-old mated female wasps (fed on drop of 20% honey/water) were exposed to different density levels of *S. cerealella* eggs. This experiment was done at 20, 25 and 30 °C, 60 ± 10% RH, and 16: 8 (L: D) photoperiod condition. To determine the effect of relative humidity on functional response of *T. brassicae*, two humidity regimes (45 ± 10% and 85 ± 10% RH) were tested at 30 °C. At least 20 replications of each density were set up, simultaneously.

After 16 hours the female parasitoids were removed and host egg were maintained under 25 ± 1 °C and 55 ± 10% RH condition. To determine the number of parasitized egg, the number of black eggs was counted. At each temperature/humidity, the wasps were reared at that condition at least for two generations and the third generation was used for experiments.

Statistical analysis

Data analysis for functional response includes two steps. In the first step, the shape (type) of functional response must be determined, typically by determining if the data fit a type II or III functional response. Logistic regression of the proportion of parasitized hosts vs. the initial number of hosts is the most effective way in determining this. In this first step, we fitted a polynomial function:

(1) $$\frac{N_a}{N_0} = \frac{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}{1+\exp(P_0 + P_1N_0 + P_2{N_0}^2 + P_3N_0^3)}$$

Where P_0, P_1, P_2, and P_3 are the parameters to be estimated. These parameters can be estimated by using the CATMOD procedure in SAS. The sign of P_1 and P_2 can be used to distinguish the shape of the curves. A positive linear parameter (P_1) and a negative quadratic parameter (P_2) indicated that functional response is type III, whereas if both parameters are negative, the functional response is type II.

After determining the type of functional response, parameters must be estimated. We used nonlinear least square regression (NLIN procedure in SAS) to estimate the parameters of the Holling's disk equation (equation 2) and Roger's (1972) random parasitoid equation (equation 3). Some authors emphasize on the limitation of Holling's disk equation, and suggest Rogers' parasite/predator equation as an alternative, which is more appropriate when prey depletion (for a predator) or reencounter (for a parasitoid) occurs during the experiment. Holling's disk equation can be used only when Rogers' model does not enable the researcher to estimate valid parameters (see Allahyari *et al*., 2004).

(2) Holling's model $N_a = aTN_0/1 + aT_hN_0$

(3) Rogers' model $$N_a = N_0\left[1-\exp\left(-\frac{aT}{1+aT_hN_0}\right)\right]$$

(4) $$a = (d + bN_0)/(1+cN_0)$$

Where N_a is the number of host attacked, N_0 the initial number of hosts, T the time of exposure (16 hours), a, the rate of successful attack, T_h the handling time and b, c, d are constant. Comparisons between parameters were performed by using an equation with indicator variables:

(5) $$N_a = N_0\left[1-\exp\left(-\frac{[b+D_b(j)]\,T\,N_0}{1+[b+D_b(j)]\,[T_h + D_{T_h}(j)]\,{N_0}^2}\right)\right]$$

Where j is an indicator variable that takes value 0 for first data set and 1 for the second data set. The parameters D_b and D_{Th} estimate the differences between the data sets in the value of the parameter b and T_h, respectively. In other words, for example the handling time for 20 °C is T_h, and for 30 °C is $T_h + D_{Th}$. For finding a difference between two handling times, it must be proved that D_{Th} is a significant amount, and it is not equal to zero. If D_{Th} is not significantly different from zero, then the difference between T_h and $T_h + D_{Th}$ is not significant and the two handling time are equal from statistical point of view (see Juliano, 2001).

Results

Functional responses of parasitoid in different conditions are illustrated in figure 1. At different temperatures *T. brassicae* showed different types of functional response. Results of a logistic regression (table 1) indicated that functional response of *T. brassica*e population at 25 °C is type II and at 20 and 30 °C is type III. At 25 °C the attack coefficient, a (0.0735 ± 0.011) and the handling time T_h (0.311 ± 0.032) were estimated from Holling's disk equation using a nonlinear least square regression.

At 20 and 30 °C, the Roger's random parasitoid equation has been used in data analysis. Equation (4) was substituted in (3) and the data set was fitted to it. Results of nonlinear least square regression indicated that parameters c and d were not significantly different from zero; therefore, we eliminated them from the model and a reduced model was used.

Estimated b value, at 20 and 30 °C were 0.0025 ± 0.0005 and 0.0046 ± 0.0007, respectively and estimated handling time (T_h) in these temperatures were 0.619 ± 0.0281 and 0.425 ± 0.0121, respectively. Estimated con-

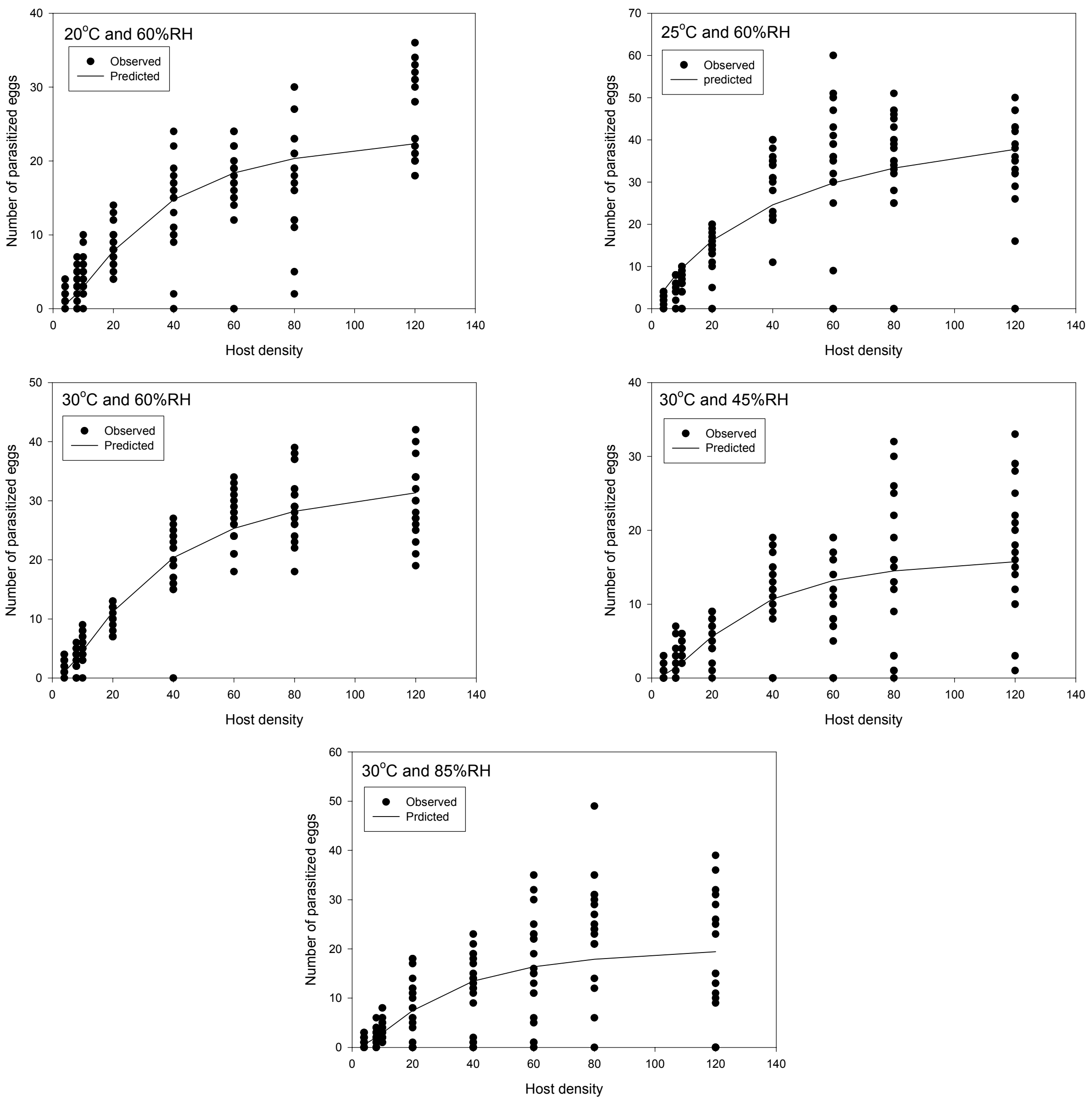

Figure 1. Functional response of *T. brassicae* to different densities of *S. cerealella* eggs, at different temperature and humidity (symbols: observed; line: predicted by model).

fidence interval for Db and D_{Th} in different data sets can be used to compare parameters b and T_h. Data analyzing by using equation 5 indicated that Db and D_{Th} are significant values; therefore, there is significant difference between b and T_h in functional response of *T. brassicae* at 20 and 30 °C (table 2).

Our results indicated that change in relative humidity at 30 °C, could not change the type of functional response of *T. brassicae* and for each two humidity, it was type III. At 45 ± 10%, estimated b value and handling time were 0.0017 ± 0.0005 and 0.906 ± 0.068, respectively. These values for 85 ± 10% RH, were 0.0025 ± 0.001 and 0.728 ± 0.06, respectively.

The outputs of model 5 showed that relative humidity changes, can not affect the values of functional response parameters of this parasitoid. Based on our results (table 2), there is not any difference in functional response of *T. brassicae* in 45% and 85% relative humidity regimes. Parameters of these two data sets were compared to the functional response of wasps in 30 °C and 60% RH. There is significant difference in functional response parameters of *T. brassicae* in 45% and 60% humidity regimes. Comparison between functional response in 60% and 85% showed that there is just significant difference in T_h value.

Discussion

A number of attributes have been proposed as characteristics of effective biological control agents; these include a high intrinsic rate of population increase, a high searching efficiency, low handling time, and a tendency to aggregate in areas where hosts are common for the target pest (Hassell, 1978). Differences in killing efficiency between two parasitoid or predator populations

Table1. Results of logistic regression analysis of the proportion of parasitized eggs by *T. brassicae*, against initial number of eggs.

Temperature / humidity	Coefficient	Estimate	SE	χ^2 Value	P value
20 °C / 60% RH	Constant	-0.00984	0.0968	0.01	0.919
"	Linear	0.0216	0.00308	48.83	<0.0001
"	Quadratic	-0.00009	0.000021	16.71	<0.0001
25 °C / 60% RH	Constant	0.1282	0.1518	0.71	0.3982
"	Linear	-0.0796	0.01	60.9	<0.0001
"	Quadratic	0.002	0.0002	82.5	<0.0001
"	Cubic	-7.7 E-6	8.9 E-7	74.45	<0.0001
30 °C / 60% RH	Constant	-0.0863	0.0936	0.85	0.356
"	Linear	0.002	0.0029	0.43	0.512
"	Quadratic	0.00007	0.00002	11.22	0.0008
30 °C / 45% RH	Constant	0.6219	0.1077	33.32	<0.0001
"	Linear	0.016	0.0035	21.24	<0.0001
"	Quadratic	-0.0005	0.0002	5.18	0.023
30 °C / 85% RH	Constant	0.4046	0.155	6.81	0.0091
"	Linear	0.0285	0.011	7.39	0.0066
"	Quadratic	-0.0005	0.0002	8.17	0.0043
"	Cubic	3.34 E-6	9.4 E-7	12.59	0.0004

Table 2. Parameters estimated by an equation with indicator variable (5) for different data set: functional response of *T. brassicae*, in different humidity regimes.

Parameter	Estimate	Asymptotic SE	Asymptotic 95% CI	
			Lower	Upper
20 °C and 30 °C				
b	0.0025	0.0005	0.0016	0.0035
T_h	0.6199	0.026	0.569	0.6711
D_b	0.00204	0.0009	0.00023	0.0038
D_{Th}	-0.1943	0.0292	-0.2518	-0.1369
45% and 60% RH				
b	0.0017	0.0005	0.00074	0.0026
T_h	0.9062	0.0588	0.7905	1.0218
D_b	0.00291	0.0009	0.0009	0.0048
D_{Th}	-0.4807	0.0606	-0.5999	-0.3614
45% and 85% RH				
b	0.0017	0.0007	0.00035	0.0029
T_h	0.9062	0.0831	0.7427	1.0697
D_b	0.0009	0.0011	-0.0013	0.003
D_{Th}	-0.1784	0.0983	-0.3719	0.0151
60% and 85% RH				
b	0.0046	0.0011	0.0024	0.0068
T_h	0.4255	0.0188	0.3885	0.4626
D_b	-0.002	0.0013	-0.0047	0.0006
D_{Th}	0.3023	0.0512	0.2015	0.4031

b: constant must be estimated.
T_h: handling time.
D_b: indicator variable estimates the differences between the humidity in the value of the parameter b.
D_{Th}: indicator variable estimates the differences between the humidity in the value of the parameter T_h.

can be compared by estimation and comparison of functional response parameters (Juliano, 2001).

This research showed that different temperature and relative humidity had a significant effect on the functional response of egg parasitoids which must be kept constant during the wasps' selection.

To determine the effect of host species on the searching efficiency, handling time and functional response of *Trichogramma embryophagum* (Hartig), it was reared on *Ephestia kuehniella* (Zeller) and *S. cerealella* eggs. In both experiments, the functional response was type III and Holling disc equation was used to estimate the parameters. The results revealed that the type of laboratory host has no important effect on the functional response of *T. embryophagum* (Fathipour *et al*., 2003). Their results encouraged us to use factitious host in this study.

In laboratory studies, finding the type I and II functional response for *Trichogramma* species is typical (Kfir, 1983; Karimiyan, 1998; Faria *et al*., 2000; Wang and Ferro, 1998; Lashgari *et al*., 2004; Mills and Lacan, 2004; Reay-Jones *et al*., 2006). Shen and Li (1987) found a linear relationship for the Asian corn borer, *Ostrinia furnacalis* (Guenée). In this research, at 25 °C, functional response trials resulted in a strong fit to a curvilinear type II response.

The type of functional response of parasitoid/predator may change from one type to another as environmental conditions (temperature mainly) change (Wang and Ferro, 1998; Mohaghegh *et al*., 2001). In our tests, data from 20 and 30 °C, fit a sigmoid type III response in which there is an initial rate of parasitisation followed by a constant rate and then a deceleration of response as in the type II model, so these two temperatures, may lead to accelerate the learning ability of female wasps and increase the rate of parasitized eggs. Difference in adaptation to different environmental condition, may be due to effects on the foraging behaviour of the parasitoids (Zhang, 1983). Gou (1986) and Zhang *et al*. (1983) suggested that changes (mainly temperature), may affect the foraging behaviour of the parasitoids. *Trichogramma* possibly possess a learning ability to discriminate parasitized eggs and unparasitized eggs through experience (Wang and Ferro, 1998) which may result in type III response. Bjorksten and Hoffmann (1998) suggested that oviposition experience had a stronger effect on host preference than pre-adult experience (learning through development in rearing host). Kaiser *et al*. (1989), suggest that females can learn to associate some olfactory cues with the presence of the host.

Our results suggested that the optimum temperature according to the highest value of a (searching ability of parasitoid) and the lowest value of T_h (handling time), was 30 °C (type III). Kalyebi *et al*. (2005), also stated that the optimum temperature for Trichogrammatid wasps was around 30 °C. Similar optimal was found for other egg parasitoids reared under constant temperature (Chabi-Olay *et al*., 2004). Furthermore some researchers found type III of functional response for *Trichogramma* species at different conditions in laboratory (Reay-Jones *et al*., 2006; Arbab Tafti *et al*., 2004).

No studies have been conducted to establish the relationship between host densities and rates of attack (functional response) for *T. brassicae* at different humidity. Although Kalyebi *et al.* (2005) evaluated the influence of relative humidity on functional response of *Trichogramma* egg parasitoid but reported humidity and its interactions with temperature and strain had no effect on the number of eggs parasitized.

Our research was done at three humidity regimes (45, 60 and 85% RH). By changing the relative humidity from 45 to 60%, wasp instantaneous searching efficiency ($a = bN_0$) increased and handling time (T_h) decreased. Increasing the relative humidity from 60 to 85% does not change the value of a significantly, but increases the T_h. This means that high relative humidity decrease the ability of the wasp. The maximum parasitism in 60 and 85% relative humidity was 37.6 and 21.9, respectively. In conclusion, high temperature and medium humidity had a strong impact on the magnitude of parasitizing capacity and thereby functional response of tested parasitoid.

The determined optimal temperature could be related to the adaptation of this species to condition of their habitat where they were collected. The optimum relative humidity in this study (60%) was very higher than the relative humidity of *Trichogramma* wasps natural habitat; therefore we can say that one of the main reasons of low wasps efficiency in Pomegranate orchards, is the low relative humidity, high relative humidity never occurred in the habitat that the specimen were collected.

In this study we could clearly establish a relationship between the functional response of *Tricogramma* wasps and temperature, although parasitoids showed high ability to perform at a wider range of humidity. Thus we can increase the parasitoid efficiency with regular irrigation and other management strategies as though the relative humidity increases at the time of *Tricogramma* release. Functional response studies in laboratory could be useful in providing the first step for comparing the efficiency of different species/strains and also provide a valid means of comparing host finding abilities of candidate natural enemies (Overholt and Smith, 1990). In addition to laboratory studies, more attention should be devoted to semi field and field condition to obtain more applicable results in the field.

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Authors' addresses: Mitra MOEZIPOUR (corresponding author, mitra_moezipour@yahoo.com), Department of Plant Protection, College of Agriculture, University of Technology, Isfahan, Iran; Maryam KAFIL (kafil@ut.ac.ir), Hossein ALLAHYARI (allahyar@ut.ac.ir), Department of Plant Protection, College of Agriculture, University of Tehran, Karaj, Iran.

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