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Functional response of six indigenous trichogrammatid egg parasitoids (Hymenoptera: Trichogrammatidae) in Kenya: influence of temperature and relative humidity

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Abstract

Laboratory tests were conducted to evaluate the functional responses of six species/strains of native Kenyan trichogrammatids using the factitious pyralid host, *Corcyra cephalonica*, under different temperature and relative humidity regimes. The objective was to identify promising species/strains for controlling the noctuid *Helicoverpa armigera*, a serious pest of vegetables in Kenya. The six species/strains of *Trichogramma* and *Trichogrammatoidea* represented collections from low (<700 m), mid (between 700 and 1200 m) and high (>1200 m) altitude locations. They were compared for parasitisation rates at six temperatures (10, 15, 20, 25, 30 and 35 °C) and two relative humidity levels (40–50% and 70–80%), at five host egg densities (6, 12, 18, 24, and 30 per adult female). Temperature affected parasitisation rates while relative humidity did not. *Trichogrammatoidea* sp. nr. *lutea* from a high altitude location, *Trichogramma* sp. nr. *mwanzai* from a low altitude site, *Trichogramma* sp. nr. *mwanzai* from a mid-altitude location and *Trichogrammatoidea*. sp. nr. *lutea* from medium altitude showed higher parasitism across a wider temperature range compared to the other strains. There was no relationship between source (altitude, climate) and performance of the strains at the temperatures and host densities tested. The implications of these results for deploying the strains for inundative biocontrol of *H. armigera* in agroecosystems in Kenya are discussed.

Keywords: Functional response; Temperature; Relative humidity; Trichogrammatids; Kenya

1. Introduction

The African bollworm *Helicoverpa armigera* is a pest of several agricultural crops in Africa (Karel, 1985; van Den berg et al., 1993). In tomatoes in Kenya, it can cause substantial direct and indirect damage leading to losses in quality and quantity amounting to 24% (ICIPE, 1997).

Trichogrammatid egg parasitoids are the most promising biological control agents for inundative releases against lepidopteran pests, including augmentative biological control of *H. armigera* in Africa (Alba, 1990; Sing and Jalali, 1994; Sithanantham et al., 2001; van Lenteren, 1983). The development of an efficient biological control program with egg parasitoids must involve selection of strains with a high efficiency against a target pest, in a given environment (Hassan, 1994; Pak, 1988). According to Hommay et al. (2002), native *Trichogramma* strains, which are generally well adapted to

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local conditions, are the favoured option for biological control of pests.

Climatic adaptation is an important criterion for selecting potential biological control agents (van Lenteren, 1986). Field-testing of natural enemies for selection for climatic adaptation can be very time consuming, especially if several candidates are involved. Hence, laboratory and greenhouse studies are useful for choosing a suitable candidate (Pak and van Lenteren, 1988).

Several biological characteristics, among them searching ability, fecundity, longevity and sex ratio, have been used to assess potential efficacy of a parasitoid. In the case of *Trichogramma*, the number of host eggs successfully parasitised by the adult female parasitoid (fecundity) after release in the field is the key attribute for selecting species or strains. Ballal and Singh (2003) evaluated the effectiveness of three species of *Trichogramma* based on fecundity. Pak and van Lenteren (1988) mentioned that strains that showed a high potential in the laboratory also have the ability to perform well in the field, while Silva et al. (2000) and Thomson and Hoffmann (2002) found no relationship between laboratory and field performance.

Another important aspect when evaluating the efficiency of a natural enemy is the attack rate across a range of densities of the host, i.e., its functional response (Berryman, 1999). The functional response is regarded as central to understanding host-parasitoid dynamics (Hassell, 1982; Houck and Strauss, 1985; Walde and Murdoch, 1988). Holling (1959, 1966) proposed three types of functional responses: type I, a linear rise to a plateau; type II, a curvilinear rise to a plateau; and type III, a sigmoid curve rising to a plateau which then levels off under the influence of handling time or satiation (Berryman, 1999; Hassell, 2000).

Weather 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 success in biological control programs has often been caused by high mortality of natural enemies due to climatic extremes. The outstanding success of *Trichogramma evanescens* Westwood to control the Asian corn borer *Ostrinia furnacalis* Guenee on the Island of Mindanaw, Philippines was partly attributed to agreeable climatic conditions (high humidity and moderate temperature) (Tran et al., 1986; Tran and Hassan, 1986). Conversely, releases of both wild and mass-reared *Psyttalia concolor* (Szépligeti), a larval parasitoid of tephritids, failed in some parts of Italy (Raspi and Loni, 1994), possibly due to poor temperature adaptation (Fenilli and Pegazzano, 1971).

The present study aimed at comparing the functional responses of six indigenous trichogrammatid species/strains under different regimes of temperature and relative humidity.

2. Materials and methods

The origins of the six species/strains of *Trichogramma* and *Trichogrammatoidea* used in the study are presented in Table 1. Among the species of *Trichogramma* were *Trichogramma* sp. nr. *mwanzai* Schulten and Feijen and *Trichogramma bruni* Nagaraja while the *Trichogrammatoidea* all belonged to *Trichogrammatoidea* sp. nr. *lutea* (Girault) They were collected in Kenya from low (L), mid (M) and high (H) altitude locations (<700, 700–1200, >1200 m, respectively). They were identified by J.C. Monje at the Institute of Phytomedicine, University of Hohenheim, Germany. The trichogrammatids were reared at the International Centre of Insect Physiology and Ecology, Nairobi, Kenya on the rice moth, *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) at 25 ± 2 °C and $50 \pm 10\%$ RH. The individuals used were from isofemale lines established from a single egg mass parasitised by a single female. Approximately equal numbers of siblings were used to start each colony. All six species/strains were recovered from *H. armigera*.

At the time of the experiment, *T.* sp. nr. *mwanzai* (M) and *T.* sp. nr. *lutea* (M) had each been in culture for six generations, *T.* sp. nr. *lutea* (L) and *T.* sp. nr. *lutea* (H) for 24, while *T. bruni* (H) and *T.* sp. nr. *mwanzai* (L) had been reared for 15 and 106 generations, respectively. The six strains were selected for their high life time fecundity among accessions from the same altitudes in a preliminary test of fecundity (Kalyebi, unpublished).

Table 1
Source of the six indigenous Kenyan trichogrammatid species used in the study

Taxon name	Site of collection	Latitude	Longitude	Elevation (m above sea level)	Min–max temperature range (°C)	Host plant
Trichogramma sp. nr. *mwanzai* (L)	Muhaka	04°19′18.1″S	39°30′24.3″E	40	23.2–32.6	Pigeon pea
Trichogrammatoidea sp. nr. *lutea* (L)	Muhaka	04°19′18.1″S	39°30′24.3″E	40	23.2–32.6	Tomato
Trichogrammatoidea sp. nr. *lutea* (M)	Kwachai	02°23′166″S	038°00′319″E	930	16.7–29.3	Tomato
Trichogramma sp. nr. *mwanzai* (M)	Mwea	00°37′464″S	037°21′801″E	1158	25–31.7	Tomato
Trichogrammatoidea sp. nr. *lutea* (H)	Muguga	01°14′590″S	036°38′236″E	2227	10.1–23	Tomato
Trichogramma bruni (H)	Muguga	01°14′590″S	036°38′236″E	2227	10.1–23	Tomato

Based on preliminary experiments on numbers attacked over 24 h (Kalyebi, unpublished), the minimum and maximum egg densities were set at 6 and 30, respectively, for tests over an 8 h period. The factitious host *C. cephalonica* was used instead of the target host *H. armigera* because of ease of rearing. Previous work has shown that the two hosts were equally suitable for all six species/strains (Muholo, 2002).

2.1. Bioassay

Five egg densities (6, 12, 18, 24, and 30 eggs per adult parasitoid) were used. For each host density, eggs were placed on a small card, using diluted adhesive gum and inserted into a glass vial (2.5 cm diameter × 7.5 cm height). A single one-day-old mated, naïve female of each of the species/strains was introduced into each glass vial and provided with minute streaks of a honey solution (200 ml honey: 100 ml distilled water: 3 g gelatin) as food. Ten replicates were conducted for each parasitoid species/strain and egg density. Glass vials containing host eggs were placed in a cage maintained at a specific relative humidity. The cage was then kept in an incubator at a set temperature (±1 °C). The temperatures used in the study were 10, 15, 20, 25, 30 and 35 °C and the relative humidity regimes were 40–50% and 70–80%. These temperatures cut across the minima and maxima, that occur in the vegetable growing areas of Kenya while the two humidities cut across altitudes and represent regimes between rainy and dry periods. Humidity was maintained according to procedures described by Hodgman (1948). Salts were placed in a container at the base of cages measuring 30 cm width × 30 cm diameter × 20 cm height. Calcium chloride (0.5 kg) was used to maintain the 40–50% RH at the lower temperatures (10, 15, 20, and 25 °C), while ammonium chloride (0.5 kg) was used for 70–80% RH. At higher temperatures (30 and 35 °C), ammonium chloride was used to maintain 40–50% RH and cotton wool (soaked in 0.2 L of water) to maintain the 70–80% RH. The cages were kept closed and sealed with vaseline. A thermo-hygrometer was placed inside the cages to monitor both temperature and humidity levels. Humidities were checked frequently and if required, adjustments were made by addition or removal of water from the salts. The photoperiod in the incubator was set at 12:12 h (L:D).

The parasitoids and eggs were held at the temperatures/humidity regimes for 8 h. After 8 h, the parasitoid wasps were killed and the egg cards kept at 25 ± 2 °C and 60–70% RH. Since selection for inundative releases was the objective of this study, the primary interest was the number of host eggs parasitised under a given climatic regime rather than the effect of temperature and humidity on parasitisation success and progeny production of a parasitoid. To determine the number of host eggs parasitised, the numbers of black eggs were counted after 2–3 days (Strand, 1986). The parasitisation (attack) rate i.e., the ratio of the number of hosts parasitised to the number available was also calculated.

2.2. Data analysis

The general linear model (PROC GLM) of SAS (SAS Institute, 2000) was used to determine which of the independent variables (temperature, RH, strain and density) significantly affected the number of eggs parasitised. The data on numbers of eggs parasitised were $\log(x+1)$ transformed before being subjected to the analysis (Sokal and Rohlf, 1981). Regression analyses were then used to determine which of the independent variables affected the number of eggs parasitised as a function of host density. The analysis was performed on subsets of the data that were pooled according to the significance of the independent variables. Linear regression (PROC REG) and non-linear regression (PROC NLIN, Levenberg–Marquardt method) were conducted on number of host eggs parasitised as a function of host density. Rogers (1972) random parasite model (Eq. (1)), which describes a type II response, was used in non-linear regression:

$$N_a = N_t[1 - \exp(aTP_t/1 + aT_hN_t)] \quad (1)$$

with N_a, the number of host eggs parasitised; N_t, the number of host eggs available; T, the total time of the experiment; P_t, the number of parasitoids; T_h, the handling time and a, the search rate.

Both linear and non-linear models were compared to determine one that best fit the data using the Akaike Information Criteria (AIC) (Sakamoto et al., 1986). Comparison of slopes was conducted using the method described by Littell et al. (1997). Comparisons between species/strains were made between 25 and 35 °C. In Kenya, tomatoes are commonly grown during the dry season under irrigation to escape diseases (M. Knapp, ICIPE, Nairobi, Kenya). Thus, the temperature range used represents means found during the rainy and the dry season (Corbett and O'Brien, 1997). However, during the dry season, mean temperatures can soar to 35 °C for a short period, which might affect performance of parasitoids released.

3. Results

Temperature and strain significantly affected the number of eggs parasitised (Table 2). Humidity and its interactions with temperature and strain had no effect on the number of eggs parasitized, thus, the data were pooled across humidity levels for subsequent analyses. Regression analyses revealed that the number of eggs parasitised did vary as a function of host density and

Table 2
Effects of independent variables and their interactions on the numbers of eggs parasitised

Source	*df*	*F* value	*P* value
Temperature	5, 3138	197.42	<0.0001
RH	1, 3138	1.83	0.1764
Strain	5, 3138	29.93	<0.0001
Temp*RH	5, 3138	0.60	0.6995
Temp*strain	25, 3138	4.43	<0.0001
RH*strain	5, 3138	1.63	0.1491

was affected by temperature ($F = 43.3$; $df = 5$, 3487; $P < 0.0001$) and species/strain ($F = 3.94$; $df = 5$, 3487; $P = 0.0015$).

Table 3 shows the slopes (parasitisation rates) and the regression statistics for each of the parasitoid species/strains at each temperature as predicted by linear regression (i.e., type I functional response). For most species/strains, the number of eggs parasitised increased with increasing host density. AIC revealed that the type I functional response gave a better fit to the data than Rogers (1972) random parasite equation (type II response) for most of the species/strains at most temperatures except for *T. bruni* (H), *T.* sp. nr. *lutea* (H), *T.* sp. nr. *lutea* (L) and *T.* sp. nr. *lutea* (M) at 10 °C and *T.* sp. nr. *mwanzai* (L) at 20 and 35 °C, for which both type I and type II fit equally well (Table 4).

For *T.* sp. nr. *mwanzai* (L), the slope, i.e., parasitisation rate, increased with increasing temperature to a maximum at 30 °C and then declined at 35 °C. The parasitisation rate at 35 °C however did not differ from that at 25 °C ($F = 0.02$; $df = 1$, 573; $P = 0.9$) (Table 3). The parasitisation rates for *T.* sp. nr. *mwanzai* (M) did not differ at 10 and 15 °C, but the rate increased between

Table 3
Linear regression estimates of the slopes (parasitisation rates) and standard errors for the proportion of host eggs parasitised by the six species/strains at initial host densities at different temperatures

Temperature (°C)	Species/strain	Estimate of slope (±SE)	*n*	*t*	*P*	R^2
10	*T.* sp. nr. *mwanzai* (L)	0.035 (0.02)	88	2.36	0.0203	0.06
	T. sp. nr. *mwanzai* (M)	0.033 (0.01)	98	3.06	0.0028	0.09
	T. sp. nr. *lutea* (M)	0.086 (0.02)	97	5.21	<0.0001	0.22
	T. sp. nr. *lutea* (L)	0.074 (0.02)	87	4.26	<0.0001	0.17
	T. sp. nr. *lutea* (H)	0.057 (0.02)	99	3.69	0.0004	0.12
	T. bruni (H)	0.018 (0.01)	95	2.64	0.01	0.07
15	*T.* sp. nr. *mwanzai* (L)	0.114 (0.02)	99	4.61	<0.0001	0.18
	T. sp. nr. *mwanzai* (M)	0.016 (0.01)	100	1.96	0.05	0.04
	T. sp. nr. *lutea* (M)	0.038 (0.01)	98	2.81	0.006	0.08
	T. sp. nr. *lutea* (L)	0.071 (0.02)	98	4.21	<0.0001	0.15
	T. sp. nr. *lutea* (H)	0.092 (0.02)	98	4.74	<0.0001	0.19
	T. bruni (H)	0.002 (0.001)	100	1.52	0.13	0.02
20	*T.* sp. nr. *mwanzai* (L)	0.241 (0.03)	100	7.31	<0.0001	0.35
	T. sp. nr. *mwanzai* (M)	0.162 (0.03)	100	5.51	<0.0001	0.23
	T. sp. nr. *lutea* (M)	0.076 (0.02)	98	4.57	<0.0001	0.18
	T. sp. nr. *lutea* (L)	0.112 (0.02)	95	5.42	<0.0001	0.24
	T. sp. nr. *lutea* (H)	0.125 (0.02)	97	5.46	<0.0001	0.24
	T. bruni (H)	0.065 (0.02)	100	3.36	0.001	0.10
25	*T.* sp. nr. *mwanzai* (L)	0.329 (0.03)	96	9.48	<0.0001	0.49
	T. sp. nr. *mwanzai* (M)	0.341 (0.03)	99	10.8	<0.0001	0.54
	T. sp. nr. *lutea* (M)	0.364 (0.03)	99	13.39	<0.0001	0.18
	T. sp. nr. *lutea* (L)	0.263 (0.03)	98	9.84	<0.0001	0.50
	T. sp. nr. *lutea* (H)	0.390 (0.03)	98	11.97	<0.0001	0.60
	T. bruni (H)	0.212 (0.03)	99	6.52	<0.0001	0.30
30	*T.* sp. nr. *mwanzai* (L)	0.513 (0.03)	98	19	<0.0001	0.79
	T. sp. nr. *mwanzai* (M)	0.435 (0.03)	95	14.87	<0.0001	0.70
	T. sp. nr. *lutea* (M)	0.501 (0.02)	100	21.28	<0.0001	0.82
	T. sp. nr. *lutea* (L)	0.414 (0.03)	98	15.6	<0.0001	0.72
	T. sp. nr. *lutea* (H)	0.444 (0.03)	98	15.77	<0.0001	0.72
	T. bruni (H)	0.237 (0.03)	99	7.46	<0.0001	0.36
35	*T.* sp. nr. *mwanzai* (L)	0.324 (0.03)	98	9.54	<0.0001	0.48
	T. sp. nr. *mwanzai* (M)	0.396 (0.02)	96	16.42	<0.0001	0.74
	T. sp. nr. *lutea* (M)	0.301 (0.03)	93	9.02	<0.0001	0.47
	T. sp. nr. *lutea* (L)	0.187 (0.03)	94	7.21	<0.0001	0.36
	T. sp. nr. *lutea* (H)	0.339 (0.03)	95	12.72	<0.0001	0.63
	T. bruni (H)	0.1 (0.02)	99	5.14	<0.0001	0.21

Table 4
Results of linear and non-linear functional response curve fits for six strains at different temperatures

Temperature (°C)	Species/strain	*n*	No. of parameters	AIC[a]-type II	AIC-type I
10	*T.* sp. nr. *mwanzai* (L)	88	2	190.11	187.49
	T. sp. nr. *mwanzai* (M)	98	2	150.20	153.38
	T. sp. nr. *lutea* (M)	97	2	232.57	232.57
	T. sp. nr. *lutea* (L)	87	2	205.42	205.42
	T. sp. nr. *lutea* (H)	99	2	226.69	226.69
	T. bruni (H)	95	2	55.37	55.37
15	*T.* sp. nr. *mwanzai* (L)	99	2	318.63	318.62
	T. sp. nr. *mwanzai* (M)	100	2	94.55	94.53
	T. sp. nr. *lutea* (M)	98	2	195.17	195.09
	T. sp. nr. *lutea* (L)	98	2	138.53	238.50
	T. sp. nr. *lutea* (H)	98	2	265.43	265.33
	T. bruni (H)	100	2	−319.91	−320.01
20	*T.* sp. nr. *mwanzai* (L)	100	2	379.62	379.62
	T. sp. nr. *mwanzai* (M)	100	2	357.59	357.57
	T. sp. nr. *lutea* (M)	98	2	229.60	229.30
	T. sp. nr. *lutea* (L)	95	2	260.27	259.47
	T. sp. nr. *lutea* (H)	97	2	296.27	296.16
	T. bruni (H)	100	2	273.45	273.40
25	*T.* sp. nr. *mwanzai* (L)	96	2	372.45	372.43
	T. sp. nr. *mwanzai* (M)	99	2	363.43	363.39
	T. sp. nr. *lutea* (M)	99	2	338.37	338.36
	T. sp. nr. *lutea* (L)	98	2	328.15	327.32
	T. sp. nr. *lutea* (H)	98	2	369.04	369.49
	T. bruni (H)	99	2	373.74	373.51
30	*T.* sp. nr. *mwanzai* (L)	98	2	335.92	329.96
	T. sp. nr. *mwanzai* (M)	95	2	339.54	336.32
	T. sp. nr. *lutea* (M)	100	2	328.87	314.95
	T. sp. nr. *lutea* (L)	98	2	348.11	325.92
	T. sp. nr. *lutea* (H)	98	2	339.68	339.49
	T. bruni (H)	99	2	364.95	364.94
35	*T.* sp. nr. *mwanzai* (L)	98	2	377.97	377.97
	T. sp. nr. *mwanzai* (M)	96	2	302.91	302.85
	T. sp. nr. *lutea* (M)	93	2	349.71	349.16
	T. sp. nr. *lutea* (L)	94	2	302.99	302.88
	T. sp. nr. *lutea* (H)	95	2	341.97	341.92
	T. bruni (H)	99	2	271.05	270.91

[a] AIC = *n*log (MSE) + 2*p* where *n* is sample size, MSE is mean square error and *p* is number of parameters. The smaller the result of AIC, the better the fit.

20 and 30 °C and then decreased at 35 °C to a rate similar to that at 25 °C ($F = 2.66$; $df = 1, 582$; $P = 0.1$). For *T.* sp. nr. *lutea* (M), the parasitisation rates at 10, 15 and 20 °C were similar; thereafter they increased with increasing temperature to a maximum at 30 °C and then decreased at 35 °C. The rate at 35 °C was lower than at 25 °C. The parasitisation rates for *T.* sp. nr. *lutea* (L) at 10 and 15 °C were similar, then increased with increasing temperature to a maximum at 30 °C and decreased at 35 °C. The rate at 35 °C was lower than at 25 °C ($F = 5.6$; $df = 1, 564$; $P = 0.02$). In the case of *T.* sp. nr. *lutea* (H), the rates at 10, 15 and 20 °C did not differ. The parasitisation rate similarly increased with increasing temperature to a maximum at 30 °C and declined at 35 °C. The rates at 25 and 35 °C were similar. For *T. bruni* (H), the rates at 10, 15 and 20 °C did not differ, the parasitisation rate increased between 20 and 30 °C and declined at 35 °C. The rate at 25 °C was higher than at 35 °C ($F = 12.89$; $df = 1, 586$; $P = 0.0004$). (Table 3).

The estimated values of parasitisation rates varied between 0.035 and 0.513 for *T.* sp. nr. *mwanzai* (L), 0.033 and 0.435 for *T.* sp. nr. *mwanzai* (M), 0.038 and 0.501 for *T.* sp. nr. *lutea* (M), 0.071 and 0.414 for *T.* sp. nr. *lutea* (L), 0.057 and 0.444 for *T.* sp. nr. *lutea* (H), and 0.018 and 0.237 for *T. bruni* (H) (Table 3).

All species/strains had maximum parasitisation rates at 30 °C (Table 3). The parasitisation rate of *T. bruni* (H) was lowest under most temperature regimes ($P < 0.0001$). At 25 °C, the parasitisation rate for *T. bruni* was lower than that of most strains except for *T.* sp. nr. *lutea* (L). At 30 °C, *T. bruni* (H) had the lowest rate at 30 °C while the other species/strains did not differ (Table 5). At 35 °C, the rate of *T.* sp. nr. *lutea* (L) was higher than that of *T. bruni* (H). These two strains however had

Table 5
Results of comparison of slopes (parasitisation rates) between species/strains at three temperatures 25, 30 and 35 °C

Species/strain	25 °C		30 °C		35 °C	
	F	*P*	*F*	*P*	*F*	*P*
T. sp. nr. *mwanzai* (L) vs. *T.* sp. nr. *mwanzai* (M)	0.08	0.78	3.83	0.05	3.40	0.07
T. sp. nr. *mwanzai* (L) vs. *T.* sp. nr. *lutea* (M)	0.65	0.42	0.09	0.77	0.32	0.57
T. sp. nr. *mwanzai* (L) vs. *T.* sp. nr. *lutea* (L)	2.19	0.14	6.32	0.01	11.5	0.0007
T. sp. nr. *mwanzai* (L) vs. *T.* sp. nr. *lutea* (H)	1.92	0.17	3.06	0.08	2.68	0.1
T. sp. nr. *mwanzai* (L) vs. *T. bruni* (H)	16.58	<0.0001	27.97	<0.0001	52.45	<0.0001
T. sp. nr. *mwanzai* (M) vs. *T.* sp. nr. *lutea* (M)	0.28	0.60	2.83	0.09	5.66	0.02
T. sp. nr. *mwanzai* (M) vs. *T.* sp. nr. *lutea* (L)	3.14	0.08	0.30	0.59	26.87	<0.0001
T. sp. nr. *mwanzai* (M) vs. *T.* sp. nr. *lutea* (H)	1.23	0.27	0.05	0.83	0.04	0.85
T. sp. nr. *mwanzai* (M) vs. *T. bruni* (H)	8.8	0.003	25.52	<0.0001	55.97	<0.0001
T. sp. nr. *lutea* (M) vs. *T.* sp. nr. *lutea* (L)	5.28	0.02	5.03	0.03	7.76	0.006
T. sp. nr. *lutea* (M) vs. *T.* sp. nr. *lutea* (H)	0.34	0.56	2.16	0.14	4.73	0.03
T. sp. nr. *lutea* (M) vs. *T. bruni* (H)	12.22	0.0005	46.36	<0.0001	25.06	<0.0001
T. sp. nr. *lutea* (L) vs. *T.* sp. nr. *lutea* (H)	8.26	0.004	0.58	0.45	24.64	<0.0001
T. sp. nr. *lutea* (L) vs. *T. bruni* (H)	1.39	0.24	20.49	<0.0001	4.63	0.03
T. sp. nr. *lutea* (H) vs. *T. bruni* (H)	16.58	<0.0001	27.97	<0.0001	52.45	<0.0001

the lowest parasitisation rates of all the strains at this temperature. Generally, apart from *T. bruni* (H) and *T.* sp. nr. *lutea* (L), four species/strains; *T.* sp. nr. *mwanzai* (L), *T.* sp. nr. *mwanzai* (M), *T.* sp. nr. *lutea* (M) and *T.* sp. nr. *lutea* (H) did not differ in parasitisation rates at these temperatures.

4. Discussion

The present study showed that temperature had a significant effect on the functional response of the egg parasitoids while relative humidity did not. These results suggest that for all parasitoids tested, the optimum temperature for maximum parasitisation was around 30 °C. Similar optima were found for developmental rates for other African egg parasitoids reared under constant temperatures (Chabi-Olaye et al., 1997, 2001, 2004). For most species/strains, the functional response was a type I. Kfir (1983) found a type II functional response for *T. pretiosum* Riley while parasitism of *Heliothis zea* (Boddie) by *Trichogramma* spp. varied from inverse density-dependent to density-dependent, depending on the distance between host eggs offered to wasps (Morrison et al., 1980); for the Asian corn borer, *O. furnacalis* (Guenee) a linear relationship was found (Shen and Li, 1987).

The existence of differences in response between species/strains in the present study suggests differences in adaptation to different temperature regimes and differences in host parasitisation abilities. Mohaghegh et al. (2001), Kfir (1983) and Wang and Ferro (1998) found that the functional response of parasitoids might change from one type to another as environmental conditions (temperatures mainly) change. Such changes may be due to effects on the foraging behaviour of the parasitoids (Guo, 1986; Zhang et al., 1983).

In the present study, a type I response generally provided the best fit to the data. Although a parasitoid with a linear response does not exhibit the theoretical potential for control of the host required for classical biological control, (Hassell et al., 1977; Hassell, 1978; Luck, 1985), the presence of a linear response is important for the continued interaction of the host and parasitoid. According to Hopper and King (1986), linear functional responses might be more common in nature than has been reported, especially when measurements are taken at realistic host densities. Wiedenmann and Smith (1993) and Sallam et al. (1999) found the functional response of *Cotesia flavipes* on *Diatrea saccharalis* and *Chilo partellus* (Lepidoptera: Pyralidae), respectively, to follow a linear response. It is important however to note that linear responses, if they genuinely occur, are linear only over a certain range of host densities. The host densities used in this study were sufficiently low that the parasitoids did not deplete the supply of eggs, and therefore a decrease in the rate of parasitisation characteristic of type II and III responses was unlikely. According to Hopper and King (1986) and Wiedenmann and Smith (1993), a linear response may be more suitable to describe functional response data than non-linear regression over a limited but realistic range of low host densities. Since a linear model generally fit the data better than the non-linear model, linear regression provides a better method for comparing the parasitoids.

Functional response studies in the laboratory have been criticised as being unnatural (Kareiva, 1990) because of the differences in the size of the area parasitoids have to search to find hosts (O'Neil, 1989). Such studies are, however, useful in providing the first step for comparing the efficiency of different species/strains (Overholt and Smith, 1990) and also provide a valid means of comparing host finding abilities of candidate natural enemies (Munyaneza and Obrycki, 1997).

In the present study, a relationship between the functional response of the parasitoids and the climate of origin could not be clearly established. Some strains showed greater plasticity in their ability to perform at different temperatures regardless of their source climatic conditions than others. For example, although *T.* sp. nr. *lutea* (H) was collected from a high altitude site (2227 m) where temperatures range between 10 and 23 °C during the tomato growing season, parasitisation rates were higher at temperatures between 30 and 35 °C than those of some strains collected from warmer areas. Because all the species/strains were stringently reared continuously as isofemale lines, there was little chance of adaptation to the laboratory environment suggesting therefore that this strain may be intrinsically superior and having a more plastic tendency for warm temperature adaptation than the others.

Four species/strains; *T.* sp. nr. *mwanzai* (L), *T.* sp. nr. *mwanzai* (M), *T.* sp. nr. *lutea* (M), and *T.* sp. nr. *lutea* (H) were found to be the most promising candidates for augmentation against *H. armigera* because of the higher parasitisation rates at the higher and extreme temperatures, which occur during the dry season, when a large portion of the tomato crop is grown.

In conclusion, temperature had a significant impact on the magnitude of parasitisation capacity and thereby functional response as demonstrated by the studied species/strains under laboratory conditions. Certainly, a more realistic estimation of the parasitoid's parasitisation behaviour will be achieved under complex field conditions. Our data suggest that for an effective inundative programme using trichogrammatids against *H. armigera*, the species/strain differences related to thermal preferences should not be ignored.

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