

# The effect of temperature and humidity on the bionomics of six African egg parasitoids (Hymenoptera: Trichogrammatidae)

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## Abstract

The life table statistics of six native Kenyan species/strains of *Trichogramma* and *Trichogrammatoidea* were established using a factitious host *Corcyra cephalonica*, Stainton (Lepidoptera: Pyralidae), at eight different temperatures (10, 15, 20, 25, 28, 30, 32 and 35°C) and two humidity levels (40–50 and 70–80%). The objective was to select insects with superior attributes for augmentative release against lepidopteran pests in horticultural crops. Both temperature and humidity affected developmental time and life table parameters of the parasitoids but temperature played a more critical role. Developmental time was inversely related to temperature. The intrinsic and finite rates of increase increased with temperature up to 30°C. Both net reproduction rate and intrinsic rate of increase were higher at the lower humidity. Temperature inversely affected generation time of parasitoid strains regardless of the relative humidity. Two strains of *Trichogramma* sp. nr. *mwanzai* collected from both low and medium altitudes and *Trichogrammatoidea* sp. nr. *lutea* from the mid-altitudes, were better adapted to both low and high temperatures than the other strains, as indicated by the high intrinsic and net reproductive rates, at both humidity levels. These three strains appear to be promising candidates for augmentation biocontrol against the African bollworm *Helicoverpa armigera* in Kenya.

**Keywords:** developmental time, life tables, temperature, humidity, egg parasitoids

## Introduction

The African bollworm *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) is a pest of several agricultural crops in Africa (Karel, 1985; van Den Berg *et al.*, 1993). It is the most common pest on vegetables especially tomatoes in Kenya (Ikin *et al.*, 1993; Farrell *et al.*, 1995).

Egg parasitoids (Hymenoptera: Trichogrammatidae) are used extensively for the control of lepidopteran pests in many areas of the world (Li, 1994). Commercial use of *Trichogramma* spp. egg parasitoids for augmentative biological control of key lepidopteran pests has been reported in over 30 countries (Wajnberg & Hassan, 1994). The effectiveness of *Trichogramma* spp. in the field depends on several factors, including its searching behaviour (habitat and host location), host preference (recognition, acceptance, suitability) and tolerance to environmental conditions (Hassan, 1994).

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Climatic tolerance of natural enemies is a key factor that determines a species' establishment and effectiveness in augmentative biological control programmes (DeBach, 1965a,b; Messenger *et al.*, 1976a,b; Hokkanen, 1985) and, thus, has been incorporated into the process of evaluating candidate natural enemies (de Jong, 1963; Kot, 1979). For inundative biological control, adaptation of natural enemies to climatic conditions prevalent during the growing season, and the ability to survive periods of extreme temperature and humidity are of primary importance.

Temperature and moisture are considered to be the most important climatic factors affecting the life history of insects (Odum, 1983) and they operate together in an interactive manner. The effects of temperature on insects are well documented. Studies have shown that temperature influences several biological characteristics of insects, including sex ratio (Godfray, 1994), adult life span, survival, fecundity and fertility (Singh & Ashby, 1985; Yang *et al.*, 1994; Dreyer & Baumgartner, 1996) and developmental rates (Taylor, 1981; Pedigo, 1989). In Kenya, the effects of temperature on development have been studied for *Trichogramma* sp. nr. *exiguum* Pinto & Platner (Ochiel, 1989), *Trichogramma bournieri* Pintureau & Babault and *Trichogramma* sp. nr. *mwanzai* Schulten & Feijen (Haile *et al.*, 2002a), and for *T. bournieri* Pintureau & Babault, *T.* sp. nr. *mwanzai* Schulten & Feijen, *T. evanescens* Westwood and *T. chilonis* Ishii (Haile *et al.*, 2002b).

Life table statistics, and especially the intrinsic rate of increase ( $r_m$ ) (Southwood, 1978), provide an excellent tool for comparing the performance of parasitoid species or strains under different climatic conditions or the quality of a host (Messenger, 1970; Orphanides & Gonzalez, 1971; Nechols *et al.*, 1989; Bleicher & Parra, 1990; Carey, 1993). A limited number of studies have examined changes in parasitoid life history characteristics as a function of both temperature and relative humidity (Messenger, 1968; Smith, 1992, 1993, 1994; Kalyebi *et al.*, 2005b). While variations in humidity may have limited influence on parasitoids in temperate zones, fluctuations in relative humidity in tropical zones such as Kenya can be drastic. Studies on the effect of humidity on arthropods are relatively scarce. In the mite *Tetranychus telarius* (Koch), the length of the incubation period of the eggs varied inversely with temperature but positively between 40–94% RH (Harrison & Smith, 1961). Similar results were found with *Oligonychus uninguis* (Jacobi) at 30–98% RH (Boyne & Hain, 1983). On the other hand, developmental period of *Tyrophagus putrescentiae* (Schrank) decreased with increasing humidity (Rivard, 1961a,b). Kalyebi *et al.* (2005a) found that relative humidity did not affect functional response of trichogrammatid egg

parasitoids in Kenya. However, both temperature and humidity significantly influenced the parasitoid's parasitization rate, longevity and progeny production (Kalyebi *et al.*, 2005b).

The present study was conducted to investigate the effect of temperature and relative humidity (RH) on the development and population growth parameters of six indigenous parasitoid species/strains. Knowledge of survival and longevity of the parasitoid under various climatic conditions may help to explain failures due to unusual weather conditions, especially extended periods of high temperatures and low humidity common in the vegetable growing zones of Kenya (Corbett & O'Brien, 1997).

## Materials and methods

Six parasitoid species/strains of *Trichogramma* and *Trichogrammatoidea* (table 1) collected from low (L), medium (M) and high (H) altitude locations (<700, <1200, >1200 m, respectively) in Kenya were used in this study. The parasitoids were reared in the laboratory at the International Center of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya on the rice moth, *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae). *Corcyra cephalonica* was used instead of *H. armigera* because of ease of rearing. Previous work has shown the two hosts to be equally suitable for development of all six species/strains (Muholo, 2002).

Developmental time was studied at eight temperatures (10, 15, 20, 25, 28, 30, 32 and 35°C) and two humidity levels (40–50 and 70–80%). Life table parameters were estimated for both humidity levels but at only five temperatures (15, 20, 25, 30 and 35°C). The temperatures used represent the range between minima and maxima conditions that occur in the vegetable growing areas of Kenya, while the two relative humidities represent differences between rainy and dry periods (Corbett & O'Brien, 1997).

## Bioassay

To determine developmental time, a 1-day-old mated female was confined in a glass vial (2.5 cm diameter × 7.5 cm height). Diet was provided in the form of minute streaks of a 10% honey/water solution on the insides of the vials. The female was then provided with an egg card containing 30 one-day-old eggs of *C. cephalonica*. The vials were placed inside rectangular acrylic cages (30 cm width × 30 cm diameter × 20 cm height) with an opening on one side, which was sealed with a sliding door. The relative humidity in the cages was maintained at either 40–50% or 70–80%. Relative humidities were adjusted as per procedures described by

Table 1. Source of the six indigenous trichogrammatid species/strains used in the study.

Taxon	Site of collection	Latitude	Longitude	Elevation (m above sea level)	Mean min/max temperature range (°C)	Mean temperature (°C)
<i>Trichogramma</i> sp. nr. <i>mwanzai</i> (L)	Muhaka	04° 19' 18.1" S	39° 30' 24.3" E	40	23.2/32.6	27.9
<i>Trichogramma</i> sp. nr. <i>mwanzai</i> (M)	Mwea	00° 37' 46.4" S	37° 21' 80.1" E	1158	25.0/31.7	28.4
<i>Trichogramma bruni</i> (H)	Muguga	01° 14' 59.0" S	36° 38' 23.6" E	2227	10.1/23.0	16.6
<i>Trichogrammatoidea</i> sp. nr. <i>lutea</i> (L)	Muhaka	04° 19' 18.1" S	39° 30' 24.3" E	40	23.2/32.6	27.9
<i>Trichogrammatoidea</i> sp. nr. <i>lutea</i> (M)	Kwachai	02° 23' 16.6" S	38° 00' 31.9" E	930	16.7/ 29.3	23.0
<i>Trichogrammatoidea</i> sp. nr. <i>lutea</i> (H)	Muguga	01° 14' 59.0" S	36° 38' 23.6" E	2227	10.1/23.0	16.6

L, M and H in parentheses indicate low, medium and high altitude, respectively.

Hodgman (1948). Salts were placed in a container (10 cm width  $\times$  10 cm diameter  $\times$  15 cm height) at the base of the cages. 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. To maintain 40–50% RH at higher temperatures (30 and 35°C), ammonium chloride (0.5 kg) was used. Cotton wool soaked in 0.2 l of water was used to maintain 70–80% RH at the two highest temperatures. The cages were kept closed and sealed with Vaseline. A thermohygrometer was placed inside each cage to monitor both temperature and humidity levels. Humidities were checked frequently and in cases of deviations from the required humidity, adjustments were made by addition or removal of water from the salts. The photoperiod was set at 12:12 (L:D).

The two RH regimes were maintained in two separate cages inside an incubator set at a particular temperature. Ten females (replicates) were assigned randomly per species/strain per temperature-humidity regime. Each day, egg cards were replaced with fresh ones until the parasitoid died. Parasitized eggs were kept at the same temperature and humidity as the adults.

Emergence was monitored every 24 h. The number of eggs parasitized, adult emergence and sex ratio (proportion of female progeny) were recorded. Daily records were kept of age specific fecundity ( $m_x$ ) and age specific longevity (survival) ( $l_x$ ) of each female (Dent & Walton, 1997) and used for constructing the life tables.

#### Statistical procedures

Differences in developmental times among parasitoid species/strains at the different temperature and humidity levels were examined by analysis of variance (ANOVA) using Proc Mixed of SAS (SAS Institute, 2000). When ANOVAs were significant, means were separated using the Lsmeans statement with the Tukey option at  $P=0.05$  (Zar, 1996).

For estimation of the lower developmental threshold and the thermal constant at the two humidity levels, a simple linear regression over the linear range of the relationship between temperature ( $T$ ) and developmental rates [ $R(T)$ ] of the egg parasitoid strains was used (Campbell *et al.*, 1974):

$$R(T) = a + bT \quad (1)$$

$R(T)$  is the inverse of developmental time, while  $a$  and  $b$  are the intercept and slope of the regression, respectively.

An attempt was also made to evaluate the effect of the vapour pressure deficit (VPD) on developmental time and survival of the parasitoids. VPD was estimated as

$$VPD = 0.61078 * \exp(17.269 * T / (T + 237.30)) (1 - RH/100) \quad (2)$$

where  $T$  is the temperature (°C) and RH is the relative humidity (Rosenberg *et al.*, 1983).

Age-specific life tables (Southwood, 1978; Bellows *et al.*, 1992) were constructed. Life table statistics were calculated using the jackknife procedure described by Hulting *et al.* (1990). Intrinsic rates of increase ( $r_m$ ) and net reproductive rates ( $R_0$ ) were compared among species/strains at the different temperature and humidity levels using Student-Newman-Keul's test based on standard errors estimated via

jackknife (Hulting *et al.*, 1990; Zar, 1996). In addition, the finite rate of increase ( $\lambda$ ) and mean generation time (GT) were used for comparing the parasitoids at the different temperature and humidity regimes.

## Results

### Development time

Both temperature and relative humidity affected the development time of the parasitoids ( $F=13463.5$ ;  $df=4,217$ ;  $P<0.0001$ ;  $F=14.5$ ;  $df=1,217$ ;  $P=0.0002$ , respectively). Significant differences in development time were also observed between species/strains ( $F=72.7$ ;  $df=5,217$ ;  $P<0.0001$ ). Similarly, the temperature  $\times$  humidity  $\times$  strain interactions were significant ( $F=2.23$ ;  $df=14,2256$ ;  $P=0.008$ ).

None of the parasitoids completed development at 10°C. At 35°C, some parasitoids completed development at the higher humidity while none survived at the lower humidity (tables 2, 3). Dissections revealed that at 10°C, parasitoids died during the pupal stage, whereas at 35°C, most parasitoids that failed to emerge died in the adult stage. Most species/strains (except *T. sp. nr. lutea* (H) and *T. bruni* (H)) successfully completed development at 35°C and 70–80% RH, but none of species/strains survived at this temperature at 40–50% RH. Differences in developmental times were observed among strains at all the temperature-humidity levels evaluated except at 25 and 28°C at 70–80% RH and at 32°C at 40–50% RH (tables 2 and 3).

At 70–80% RH at 15°C, *T. sp. nr. mwanzai* (M) had the longest developmental time. *Trichogrammatoidea sp. nr. lutea* (M) had the shortest and *T. sp. nr. lutea* (L) had the longest developmental time at 20°C. *Trichogramma bruni* (H) did not complete development at 35°C (table 2).

At 40–50% RH, *T. sp. nr. mwanzai* (M) had the longest developmental time at 15°C while *T. bruni* (H) did not complete development at this temperature. *Trichogrammatoidea sp. nr. lutea* (M) had the shortest developmental time at 20°C, and *T. sp. nr. lutea* (H) had the longest at 30°C.

In general, parasitoid developmental time was inversely related to temperature, regardless of humidity. *Trichogrammatoidea sp. nr. lutea* (H) and (L), and *T. sp. nr. mwanzai* (M) developed faster at 40–50% RH than at 70–80% RH at 15 and 20°C. At 28°C, all strains with the exception of *T. sp. nr. lutea* (L) and *T. bruni* (H) had longer developmental times at 70–80% RH than at 40–50% RH while at 32°C, *T. sp. nr. mwanzai* (L), *T. sp. nr. mwanzai* (M) and *T. sp. nr. lutea* (M) had shorter developmental times at 40–50% RH.

The lower developmental thresholds (LTH) calculated from the linear regression of temperature ( $T$ ) on developmental rate (equation 1) and the number of degree-days (DD) required for successful development by the six species/strains at the two humidity levels are shown in table 4. The LTH was higher at the lower than at the higher humidity for most species/strains except for *T. sp. nr. lutea* (H) and *T. sp. nr. lutea* (M). There was no clear relationship between source (altitude/temperature) of the parasitoid and its LTH, at both humidity levels.

There was a significant interaction of VPD and strain on developmental time ( $F=20.58$ ;  $df=5,401$ ;  $P<0.0001$ ). Generally, developmental time decreased with an increase in VPD (fig. 1). VPD also significantly affected age-specific fecundity, which increased to a VPD of 1.06 hPa at the higher humidity and 2.33 hPa at the lower humidity level ( $F=132.1$ ;

Table 2. Mean ( $\pm$ SE) developmental time (days) of six trichogrammatid species/strains at different temperatures at 70–80% relative humidity.

Temperature (°C)	<i>T. sp. nr. lutea</i> (L)	<i>T. sp. nr. mwanzai</i> (L)	<i>T. sp. nr. lutea</i> (H)	<i>T. brunii</i> (H)	<i>T. sp. nr. mwanzai</i> (M)	<i>T. sp. nr. lutea</i> (M)	F	df	P
15	27.5 $\pm$ 0.5b A	25.3 $\pm$ 0.2d A	25.8 $\pm$ 0.2cd A	26.0 $\pm$ 0.0c A	30.0 $\pm$ 0.0a A	25.0 $\pm$ 0.0d A	105.7	5,20	<0.0001
20	14.0 $\pm$ 0.0a B	12.8 $\pm$ 0.1b B	13.0 $\pm$ 0.0b B	13.0 $\pm$ 0.0b B	13.0 $\pm$ 0.0b B	12.3 $\pm$ 0.2c B	16.9	5,31	<0.0001
25	10.0 $\pm$ 0.0 C	9.6 $\pm$ 0.2 C	9.9 $\pm$ 0.1 C	10.0 $\pm$ 0.0 C	9.8 $\pm$ 0.02 C	10.00.0 C	0.88	5,25	0.51
28	9.0 $\pm$ 0.3 CD	9.3 $\pm$ 0.2 C	9.0 $\pm$ 0.0 D	9.0 $\pm$ 0.0 D	9.6 $\pm$ 0.2 C	9.1 $\pm$ 0.1 D	1.81	5,44	0.13
30	9.2 $\pm$ 0.4a CD	8.0 $\pm$ 0.0b D	8.0 $\pm$ 0.0b E	9.0 $\pm$ 0.0a D	8.0 $\pm$ 0.0b D	8.0 $\pm$ 0.0b E	19.6	5,44	<0.0001
32	9.3 $\pm$ 0.2a CD	8.2 $\pm$ 0.1b D	8.1 $\pm$ 0.1b E	9.0 $\pm$ 0.0a D	8.1 $\pm$ 0.1b D	8.2 $\pm$ 0.2b E	13.1	5,43	<0.0001
35	8.0a D	8.0a D	ND	ND	8.0a D	8.0a E			
F	40.73	1817	4306.4		3423.8	1591.4			
df	6,28	6,49	5,41	5,18	6,40	6,36			
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001			

Means followed by the same lower case letter within row and followed by the same upper case letter within column are not significantly different at  $P=0.05$  (Tukey test). ND, no completion of development.

Table 3. Mean ( $\pm$ SE) developmental time (days) of six trichogrammatid species/strains at different temperatures at 40–50% relative humidity.

Temperature (°C)	<i>T. sp. nr. lutea</i> (L)	<i>T. sp. nr. mwanzai</i> (L)	<i>T. sp. nr. lutea</i> (H)	<i>T. brunii</i> (H)	<i>T. sp. nr. mwanzai</i> (M)	<i>T. sp. nr. lutea</i> (M)	F	df	P
15	28.0 $\pm$ 0.0b A	25.7 $\pm$ 0.3c A	25.0 $\pm$ 0.0c A	ND	29.8 $\pm$ 0.3a A	25.0 $\pm$ 0.0c A	45.1	4,12	<0.0001
20	13.0 $\pm$ 0.0a B	12.9 $\pm$ 0.1a B	12.7 $\pm$ 0.2a B	13.0 $\pm$ 0.0a A	12.9 $\pm$ 0.1a B	12.0 $\pm$ 0.0b B	6.76	5,30	0.0003
25	10.0 $\pm$ 0.0a C	8.8 $\pm$ 0.05cd C	8.9 $\pm$ 0.05c C	10.4 $\pm$ 0.04a B	9.3 $\pm$ 0.04b C	8.6 $\pm$ 0.04d C	5.79	5,30	0.0007
28	9.0 $\pm$ 0.1a C	8.1 $\pm$ 0.1b E	8.1 $\pm$ 0.1b D	10.14 $\pm$ 0.1a B	8.3 $\pm$ 0.3b DE	8.1 $\pm$ 0.1b E	65.26	5,43	<0.0001
30	8.5 $\pm$ 0.3b D	8.0 $\pm$ 0.0c E	9.0 $\pm$ 0.0a D	8.0c C	8.0c E	8.7 $\pm$ 0.1b E	10.1	5,29	<0.0001
32	8.9 $\pm$ 0.1 D	8.7 $\pm$ 0.2 D	8.4 $\pm$ 0.2 D	8.8 $\pm$ 0.2 C	8.7 $\pm$ 0.2 CD	9.0 $\pm$ 0.0 D	2.32	5,45	0.06
35	ND	ND	ND	ND	ND	ND			
F	1318.3	1550.7	1757.4	47.69	2082.76	947.66			
df	5,27	5,44	5,40	4,12	5,34	5,32			
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001			

Means followed by the same lower case letter in each row and those followed by the same upper case letter in each column are not significantly different at  $P=0.05$  (Tukey test). ND, no completion of development.

df=9,5045;  $P<0.0001$ ). Although VPD had a significant influence on age-specific survivorship ( $F=241.6$ ; df=9,5045;  $P<0.0001$ ), there were no clear trends.

#### Life table parameters

##### Net reproductive rate ( $R_0$ )

At 70–80% RH, the highest  $R_0$  for *T. sp. nr. lutea* (L) was found at 30°C (table 5). The population multiplied 15.9 times in 9.1 days. At 40–50% RH,  $R_0$  did not differ significantly between 20 and 30°C (table 6). *Trichogramma sp. nr. mwanzai* (L) had the highest  $R_0$  at 25°C at the two humidity levels. *T. sp. nr. lutea* (H) had the lowest  $R_0$  at 15°C at 70–80% RH while  $R_0$  did not differ between 20 and 30°C. At 40–50% RH,  $R_0$  at 20 and 30°C were higher than at 15°C. For *T. brunii* (H),

Table 4. Lower temperature thresholds (LTH) and degree-days (DD) for the six trichogrammatid species/strains at two humidity levels as calculated from linear regression.

Species/strain	70–80% RH		40–50% RH	
	LTH (°C)	DD	LHT (°C)	DD
<i>T. sp. nr. lutea</i> (L)	8.9	158.0	8.3	161.1
<i>T. sp. nr. mwanzai</i> (L)	8.6	153.0	9.1	149.9
<i>T. sp. nr. lutea</i> (H)	8.2	161.0	9.1	142.9
<i>T. brunii</i> (H)	7.7	172.0	11.6	400.0
<i>T. sp. nr. mwanzai</i> (M)	9.5	147.0	10.7	142.9
<i>T. sp. nr. lutea</i> (M)	7.5	169.5	6.4	169.5

there were no significant differences in  $R_0$  between 15 and 30°C at 70–80% RH but it was highest at 20°C at 40–50% RH. *Trichogramma sp. nr. mwanzai* (M) had the maximum increase

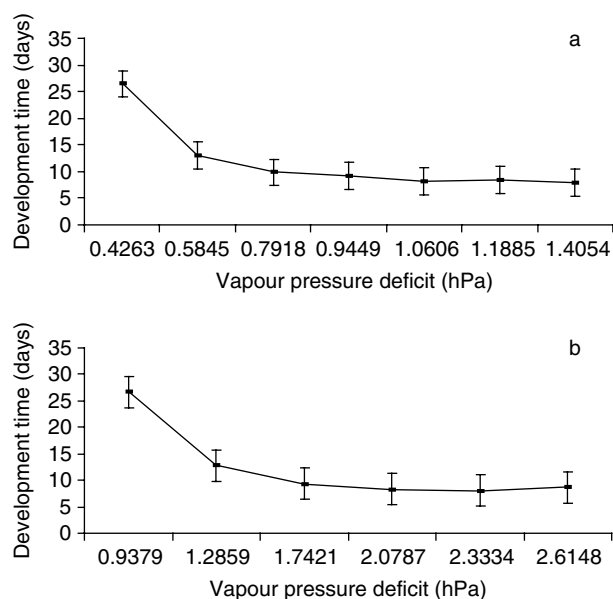


Fig. 1. Relationship between developmental time of parasitoid species/strains and vapour pressure deficit at (a) 70–80% and (b) 40–50% relative humidity.

in capacity at 25°C at 70–80% RH (table 5) and the lowest at 15°C at 40–50% RH (table 6). The generational increase at 30°C was higher than at 20°C. For *T. sp. nr. lutea* (M), the highest  $R_0$  occurred between 25 and 30°C at both humidity levels, and it was higher at 20 and 25°C than at 15°C.

At each temperature, significant differences in  $R_0$  were observed between parasitoid species/strains at the two humidity levels (tables 5 and 6). At 70–80% RH at 35°C, *T. bruni* (H) and *T. sp. nr. lutea* (H) did not survive. Similarly, at 40–50% RH at 15°C, *T. bruni* (H) did not survive while at 30°C, *T. sp. nr. mwanzai* (M) had the highest  $R_0$ . At 35°C, no species/strains survived at 40–50% RH. Generally,  $R_0$  for most parasitoid strains were higher between 25°C and 30°C than at other temperatures.

*Intrinsic rate of natural increase (r<sub>m</sub>)*

At both humidity regimes, the highest  $r_m$  for most strains was reached at 30°C except for *T. sp. nr. mwanzai* (M) at 70–80% and *T. sp. nr. mwanzai* (L) at 40–50%, which produced the highest  $r_m$  at 25°C, (fig. 2). At 30°C, *T. sp. nr. mwanzai* (M) had the highest  $r_m$  while at 35°C, all species/strains died.

The finite rate of increase also followed the same trend (fig. 3). Generation time, on the other hand, was negatively related to temperature (fig. 4). In many cases, the  $R_0$  and  $r_m$  were higher at the lower than the higher humidity level (tables 5, 6 and fig. 2). Trends of  $r_m$ , GT,  $\lambda$  and  $R_0$  with VPD were similar to those observed with temperature at the two relative humidities.

**Discussion**

In the present study, temperature was more important for parasitoid development and reproduction than humidity, and the trends were similar at both humidity levels. Several

Table 5. Net reproductive rate ( $R_0 \pm SE$ ) of six trichogrammatid species/strains at different temperatures at 70–80% relative humidity.

Temperature (°C)	<i>T. sp. nr. lutea</i> (L)	<i>T. sp. nr. mwanzai</i> (L)	<i>T. sp. nr. lutea</i> (H)	<i>T. bruni</i> (H)	<i>T. sp. nr. mwanzai</i> (M)	<i>T. sp. nr. lutea</i> (M)
15	4.2 ± 1.4ab B	9.4 ± 2.4c C	1.9 ± 0.9a A	7.2 ± 2.7bc A	9.2 ± 2.2c B	3.6 ± 0.9ab A
20	7.6 ± 2.2bc BC	2.3 ± 0.9a A	6.6 ± 1.7b B	6.7 ± 2.5bc A	10.8 ± 2.2c B	7.6 ± 2.9bc A
25	8.3 ± 2.5a C	15.9 ± 3.9b D	5.6 ± 1.2a B	6.6 ± 1.3a A	25.7 ± 3.0c C	16.9 ± 4.3b B
30	15.9 ± 4.3b D	8.5 ± 2.8a BC	8.9 ± 2.5a B	6.8 ± 2.4a A	8.6 ± 1.5a B	22.8 ± 4.6b B
35	1.7 ± 0.3a A	4.7 ± 1.1b B	–	–	2.2 ± 2.2ab A	4.9 ± 4.8b A

Means followed by the same lower case letter in each row and those followed by the same upper case letter in each column are not significantly different ( $P=0.05$ ) (Student-Newman-Keul’s test).

Table 6. Net reproductive rate ( $R_0 \pm SE$ ) of six trichogrammatid species/strains at different temperatures at 40–50% relative humidity.

Temperature (°C)	<i>T. sp. nr. lutea</i> (L)	<i>T. sp. nr. mwanzai</i> (L)	<i>T. sp. nr. lutea</i> (H)	<i>T. bruni</i> (H)	<i>T. sp. nr. mwanzai</i> (M)	<i>T. sp. nr. lutea</i> (M)
15	6.9 ± 1.6a A	9.2 ± 2.6a AB	5.7 ± 1.44a A	–	18.0 ± 3.2b A	9.1 ± 3.7a A
20	20.7 ± 3.9ab B	14.4 ± 3.8ab B	13.3 ± 3.1a B	13.8 ± 3.8a B	32.3 ± 4.5c B	21.5 ± 3.8b B
25	8.3 ± 2.6a A	31.7 ± 4.8b C	9.6 ± 3.2a AB	6.5 ± 1.9a A	39.6 ± 4.5c BC	23.2 ± 3.8b B
30	23.3 ± 5.3c B	5.8 ± 1.9a A	11.2 ± 1.4b B	6.7 ± 3.1ab A	46.7 ± 4.6d C	16.2 ± 3.3c AB

Means followed by the same lower case letter in each row and those followed by the same upper case letter in each column are not significantly different ( $P=0.05$ ) (Student-Newman-Keul’s test).



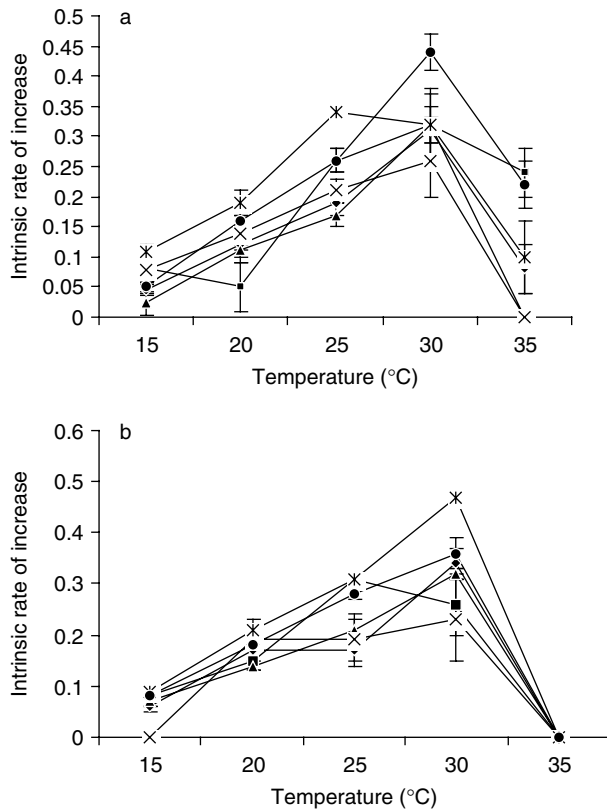


Fig. 2. Intrinsic rate of increase ( $r_m$ ) of six trichogrammatid species/strains at (a) 70–80% and (b) 40–50% relative humidity.  $\blacklozenge$ , *Trichogrammatoidea* sp. nr. *lutea* (L);  $\bullet$ , *T.* sp. nr. *lutea* (M);  $\blacktriangle$ , *T.* sp. nr. *lutea* (H);  $\blacksquare$ , *Trichogramma* sp. nr. *mwanzai* (L);  $\times$ , *T.* sp. nr. *mwanzai* (M);  $\times$ , *Trichogramma* *bruni*; L, low altitude; M, medium altitude; H, high altitude.

authors have shown that among physical factors, temperature exerts the strongest influence on the biological characteristics of *Trichogramma* (van den Bosch & Messenger, 1973; Noldus, 1989; Dent, 1991; Pratissoli, 1995). In general, insects develop faster at higher temperatures (Wagner *et al.*, 1984) but optima, maxima and minima differ among species and have important consequences for parasitoid performance in the field.

A few studies have reported the effects of relative humidity on the life history of parasitoids. These reports tend to support the conclusion that relative humidity has little effect on immature and adult survivorship, fecundity or progeny sex ratio, except under extreme humidity or temperature conditions. For example, mortality of immatures of *Trichogramma pretiosum* Riley changed little in the range 40–80% RH, but increased substantially at 10 or 100% RH (Gross, 1988). Mortality of immature *Telenomus remus* Nixon (Scelionidae) decreased at 25% RH (Gautam, 1986), whereas that of *T. reynoldsi* Gordh & Coker, was affected by RH only at extreme temperatures (18 or 33–35°C) (Cave & Gaylor, 1988).

Adult survivorship of the braconid *Chenus inanitus* (Linnaeus) (Rechav, 1978) and the eulophids *Tetrastichus pyrillae* Crawford (Yadav & Chaudhary, 1987) and *Ooencyrtus papilionis* Ashmead (Rahim *et al.*, 1991) was not affected

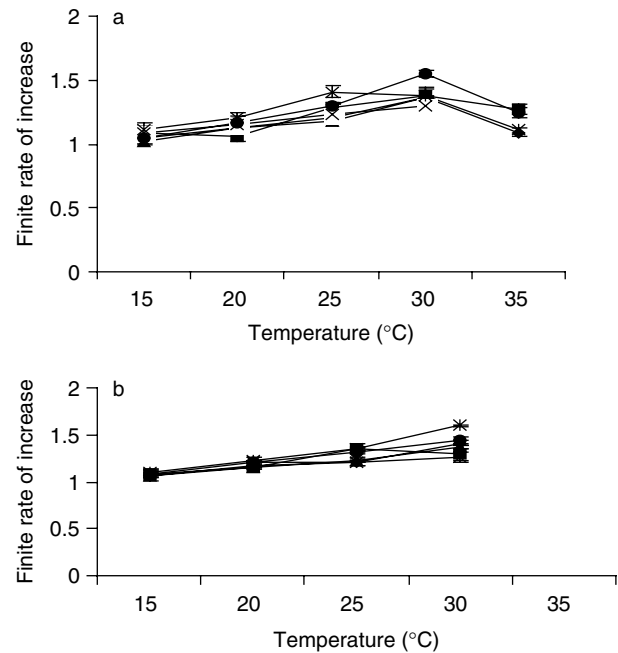


Fig. 3. Finite rate of increase ( $\lambda$ ) of six trichogrammatid species/strains at different temperatures at (a) 70–80% and (b) 40–50% relative humidity.  $\blacklozenge$ , *Trichogrammatoidea* sp. nr. *lutea* (L);  $\bullet$ , *T.* sp. nr. *lutea* (M);  $\blacktriangle$ , *T.* sp. nr. *lutea* (H);  $\blacksquare$ , *Trichogramma* sp. nr. *mwanzai* (L);  $\times$ , *T.* sp. nr. *mwanzai* (M);  $\times$ , *Trichogramma* *bruni*; L, low altitude; M, medium altitude; H, high altitude.

by RH, but longevity of *T. remus* decreased at 25% (Gautam, 1986). RH did not affect fecundity or progeny sex ratio of *Cheiloneurus pyrillae* Mani, an encyrtid egg parasitoid (Yadav & Chaudhary, 1988).

Developmental time appears to be affected more consistently by RH than the life history characters mentioned above. Calvin *et al.* (1984) found that *T. pretiosum* development was prolonged and adult fecundity was reduced at relative humidities as low as 20%. According to Yadav & Chaudhary (1986) and Cave & Gaylor (1988) development time decreases slightly, but significantly, with increasing RH. This was also evident in the present study although developmental time varied with both temperature and species/strain. The physiological reason why developmental time increases at low RH is not known but may be related to decreasing rates of feeding (Boudreaux, 1958; Corbet, 1968) or enzymatic reactions at sub-optimal osmotic conditions. Willmer (1982) has also suggested that evaporative cooling associated with transpiration could cause a decrease in body temperature with decreasing humidity, resulting in increased energy costs for maintaining water balance and this may result in increased developmental time (Willmer, 1982).

Among the life history parameters, only developmental time was affected by VPD; it decreased with increasing VPD (fig. 1).

The optimum temperatures for development of the trichogrammatid egg parasitoid species/strains in the present study appear to be around 30°C. This is consistent with the value of 30°C found for the same species/strains by

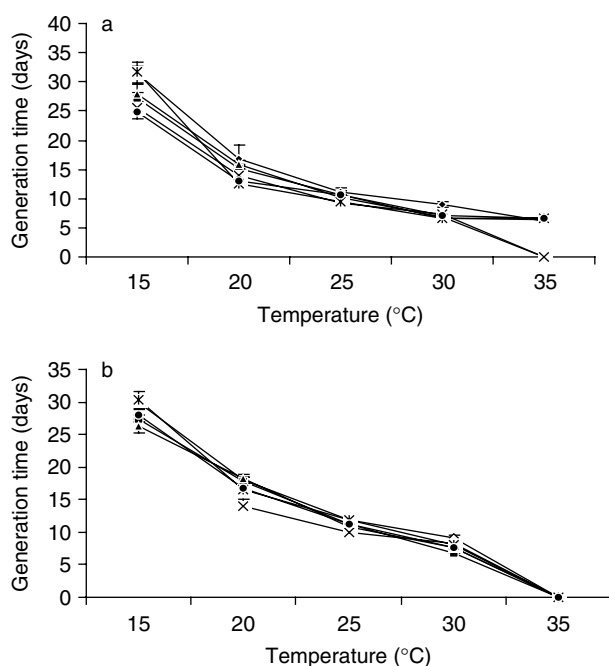


Fig. 4. Generation time (GT) of six species/strains at different temperature regimes at (a) 70–80% and (b) 40–50% relative humidity. ◆, *Trichogrammatoidea* sp. nr. *lutea* (L); ●, *T. sp. nr. lutea* (M); ▲, *T. sp. nr. lutea* (H); ■, *Trichogramma* sp. nr. *mwanzai* (L); ✱, *T. sp. nr. mwanzai* (M); ✕, *Trichogramma bruni*; L, low altitude; M, medium altitude; H, high altitude.

Kalyebi *et al.* (2005a) and for other African egg parasitoids (Chabi-Olaye *et al.*, 2001, 2004). The lower temperature thresholds obtained from this study are comparable to those observed for other trichogrammatid species, such as 8.8 and 9.2°C for *T. chilonis* and *T. evanescens*, respectively (Haile *et al.*, 2002a), and 9.9°C for *T. cacoeciae* Marchal (Uzun & Akten, 1992), but they were considerably lower than the *c.* 14°C calculated for other tropical egg parasitoid species (Chabi-Olaye *et al.*, 1997, 2001, 2004). At 10°C, there was some development though none of the parasitoids reached the adult stage. Thus, it can be expected that the temperature where development was initiated was below 10°C. There is no information on the lower temperature thresholds for *H. armigera* in Africa. Outside the tropics, for example in China, temperature thresholds for egg, larval and pupal stages have been estimated to be 9.4, 12.3 and 14.2°C with heat sums of 31.54, 200.78 and 127.6 degree-days, respectively (Li *et al.*, 1987).

According to Pak & Oatman (1982) and Tsai & Wang (1999), the true influence of temperature on population growth is reflected in the  $r_m$  values, which is the result of development, survival and reproduction. At the lowest temperature of 15°C, at both humidity levels, the species/strains exhibited comparatively low  $r_m$  values (fig. 2) as a result of prolonged development of the immature parasitoid, whereas at extremely high temperature, low  $r_m$  values were mainly due to low survival (tables 2 and 3). The lower humidity regime adversely affected the species/strains at the highest temperature resulting in no parasitoid emergence. Desiccation was a probable cause of death at higher

temperatures at the lower humidity. In Kenya, high temperatures combined with low humidity are common during the dry season and at such times, crops such as tomatoes are grown under irrigation which enables them to escape diseases (M. Knapp, ICIPE, Nairobi, Kenya, personal communication).

The  $r_m$  values for *T. sp. nr. mwanzai* (L) and *T. sp. nr. mwanzai* (M), at both humidity levels at 25°C, compare well with the 0.309 obtained by Haile *et al.* (2002b) for the same species at 26±1°C and 70±10% RH. These were also comparable to the value of 0.30 obtained for *Trichogrammatoidea baetrae* Nagaraja at 30°C (Malik, 2001). *Trichogramma* sp. nr. *mwanzai* (L), *T. sp. nr. mwanzai* (M) and *Trichogrammatoidea* sp. nr. *lutea* (M) were better adapted to both low and high temperatures at both humidity levels than the other species as indicated by their high intrinsic rate of increase. In an earlier study, the same species/strains exhibited highest survival, fecundity and progeny production (Kalyebi *et al.*, 2005b). There was no clear relationship between the performance of a strain and the climate from where it was originally collected. However, because of a lower developmental threshold, some strains from the lower and medium altitudes appear to have a wider thermal tolerance than other strains.

Several authors have used life tables to compare strains and/or species of *Trichogramma*. Bleicher & Parra (1990) evaluated the development of three populations of *Trichogramma* collected from *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae) and identified differences between these populations using life table parameters. Similarly, Maceda *et al.* (1994) compared *Trichogramma pretiosum* and *Trichogramma annulata* De Santis using the finite ratio of increase ( $\lambda$ ). More recently, Haile *et al.* (2002b) used the intrinsic and net reproductive rates to establish if there were physiological differences between *T. sp. nr. mwanzai* and *T. bournieri* from Kenya. In the present study, *T. sp. nr. mwanzai* (M), *T. sp. nr. mwanzai* (L) and *T. sp. nr. lutea* (M) were superior to the others as indicated by their superior performance and adaptation to the range of temperatures and humidities tested. While current efforts are targeting inundative releases, there is growing interest in not only what the released parasitoids will do but also the impact of their progeny, i.e. in an inoculative approach. In developing augmentative release programme strategies for these parasitoids, the present results suggest that temperature and humidity may affect the development and reproductive capacities of the released parasitoids. Because relative humidity within a plant canopy or leaf surface is a function of many variables, including wind turbulence, leaf and canopy architecture and ambient conditions (Cloudsley-Thompson, 1962; Wilmer, 1986), the relative humidity experienced by the parasitoids on the surface of a tomato plant would be expected to change significantly throughout the season depending on irrigation practices and weather patterns. Further studies on humidity-related effects on parasitoids including measurements of relative humidity or vapour pressure on plant surface may be needed.

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