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Parasitism, longevity and progeny production of six indigenous Kenyan trichogrammatid egg parasitoids (Hymenoptera: Trichogrammatidae) at different temperature and relative humidity regimes

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Abstract
Six native Kenyan species/strains of *Trichogramma* and *Trichogrammatoidea*, recovered from *Helicoverpa armigera* were evaluated at six different temperatures (10, 15, 20, 25, 30 and 35°C) and two relative humidity levels (40–50 and 70–80%) with the aim of selecting strains adapted to warmer temperature regimes. The species/strains were collected from low (<700 m), medium (between 700 and 1200 m) and high altitude (>1200 m) locations and were evaluated for parasitism, adult longevity, progeny production and progeny sex ratio at the different environmental regimes. Eggs of the factitious host, *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae) were used in the investigations. Temperature and humidity interactions affected parasitism and progeny production. The highest parasitism at the two humidity levels was at 25 and 30°C for all the strains evaluated. Adult longevity was also significantly affected by the interaction of temperature and relative humidity and was longer at the lower than higher relative humidity. Survival followed a type I survivorship curve at lower temperatures and a type III survivorship curve at the higher temperatures. *Trichogramma* sp. nr. *mwanzai* from low altitude, *Trichogramma* sp. nr. *mwanzai* from medium altitude and *Trichogrammatoidea* sp. nr. *lutea* also from medium altitude lived longer than other strains at all the temperatures and relative humidity levels evaluated, including the warmest regimes of 30 and 35°C. These strains appear promising as candidates for augmentative biocontrol of *H. armigera* in Kenya.

Keywords: *Parasitism, progeny, longevity, trichogrammatids, Kenya*

Introduction

Egg parasitoids of the genus *Trichogramma* have been used as inundative biological control agents against a range of agricultural pests, mainly lepidopterans (Li 1994; van Lenteren 2000) in a variety of agroecosystems (Hassan & Guo 1991; Pinto & Stouthamer 1994). Information on the biology of *Trichogrammatoidea* spp. is more

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limited, although several species are considered to be important natural enemies of agricultural pests in various parts of the world (Nagaraja 1978).

The African bollworm, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) is a key pest of tomato in Kenya (Farrell et al. 1995) and an important constraint in vegetable-based cropping systems in Africa (Ikin et al. 1993), where it is active throughout the year but often becomes more important during warmer seasons. Several native trichogrammatid species occur in Kenya and elsewhere in Africa on this pest (Sithanantham et al. 2001). For efficient use, a choice of better-adapted species/strains based on a thorough understanding of their biology is important. The efficiency of parasitoids in the field is affected by adverse climatic conditions (Gupta 1956; Messenger 1970). The ability of each species (and sometimes each population) to cope with fluctuating environmental conditions in the target area is an important factor affecting their impact in field situations. According to Hassan (1994) and Voegele (1988), indigenous trichogrammatids tend to be better adapted to local climates, habitat and host conditions than exotic ones.

Trichogramma spp. are particularly suitable for use as a 'biotic pesticide' through inundative releases (van Lenteren 1983) and number of host eggs successfully parasitised by the adult female parasitoid within her life time (fecundity) after release in the field, is the key attribute for selecting species/strains. The performance of a parasitoid in its intended role after release is an important attribute of its quality (Bigler 1994; Smith 1996). Life history traits (progeny production/sex ratio) are secondary and are important only as efficiency parameters in mass production and hence of limited importance in selecting for an inundative system.

In the present study, the effect of temperature and relative humidity on parasitism, adult longevity, progeny production and sex ratio of six indigenous trichogrammatid species/strains was evaluated to select the best adapted strains for augmentative control of *H. armigera*. The study particularly aimed at finding strains better adapted to higher temperatures, which are generally encountered in pest-prone areas/seasons.

Materials and methods

The methodologies adopted were similar to those employed by Liu and Smith (2000) in comparing *Trichogramma* adults from accessions (inbred lines) assembled from surveys of eggs of the target pest, *Choristoneura fumiferana* (Clemens) for their fecundity and longevity. The test candidate was reared for several generations on the factitious host, *Ephestia kuehniella* Zeller. *Trichogramma* accessions were compared for their parasitisation efficiency in the laboratory as the basis for identifying promising candidates for field release for biocontrol of the target pest.

Source location of species/strains

The origins of the six species/strains of native *Trichogramma* and *Trichogrammatoidea* used in the study are presented in Table I. They were collected from low (ex. low altitude), medium (ex. medium altitude) and high (ex. high altitude) altitude locations ($<$700, 700–1200, $>$1200 m, respectively) in Kenya. The species/strains were identified by J.C. Monje at the Institute of Phytomedicine, University of Hohenheim (Germany). The individuals used were from isofemale lines established from a single egg mass parasitised by a single female. Approximately equal numbers of siblings were

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

Taxon name	Collection site	Latitude	Longitude	Elevation (m above sea level)	Min–Max temperature range (°C)
Trichogramma sp. nr. *mwanzai* (ex. low altitude)	Muhaka	04° 19′ 18.1″ S	39° 30′ 24.3″ E	40	23.2–32.6
Trichogramma sp. nr. *mwanzai* (ex. medium altitude)	Mwea	00° 37′ 464″ S	037° 21′ 801″ E	1158	25–31.7
Trichogramma bruni (ex. high altitude)	Muguga	01° 14′ 590″ S	036° 38′ 236″ E	2227	10.1–23
Trichogrammatoidea sp. nr. *lutea* (ex. low altitude)	Muhaka	04° 19′ 18.1″ S	39° 30′ 24.3″ E	40	23.2–32.6
Trichogrammatoidea sp. nr. *lutea* (ex. medium altitude)	Kwachai	02° 23′ 166″ S,	038° 00′ 319″ E	930	28–30
Trichogrammatoidea sp. nr. *lutea* (ex. high altitude)	Muguga	01° 14′ 590″ S	036° 38′ 236″ E	2227	10.1–23

used to start each colony. All six species/strains were recovered from *H. armigera* and were reared on the rice moth, *Corcyra cephalonica* Stainton (Lepidoptera: Pyralidae). At the time of the experiment, *T.* sp. nr. *mwanzai* (ex. medium altitude) and *Trichogrammatoidea* (*To*). sp. nr. *lutea* (ex. medium altitude) had each been in culture for six generations, *To*. sp. nr. *lutea* (ex. low altitude) and *To*. sp. nr. *lutea* (ex. high altitude) for 24, while *T. bruni* (ex. high altitude) and *T.* sp. nr. *mwanzai* (ex. low altitude) had been reared for 15 and 106 generations, respectively. The factitious host *C. cephalonica* was used instead of the target host *H. armigera* in testing the responses because of ease of rearing. Previous work has shown that the two hosts were equally suitable for all six species/strains (Muholo 2002).

Bioassay

Freshly emerged 1-day-old mated females were provided with fine streaks of 10% honey solution in glass vials. Ten females per strain were used as replicates for each temperature/humidity regime. They were individually confined in glass vials (2.5 × 7.5 cm) and provided with honey solution. The glass vials were placed inside acrylic cage (30 × 30 × 20 cm, width × diameter × height) maintained at a specific relative humidity, which was then placed inside an incubator at a set temperature (±1°C) for 24 h. The temperatures used in the evaluations were 10, 15, 20, 25, 30 and 35°C and there were two humidity levels (40–50 and 70–80%). These temperatures represent the minima and maxima that occur in the vegetable growing areas of Kenya while the two humidities represent differences between rainy seasons and dry periods.

Humidity was maintained according to the procedures described by Hodgman (1948). Calcium chloride (0.5 kg) was used to maintain a 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 salts were placed in a container at the base of the cages. The cages were kept closed and the lids were 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).

Eggs of *C. cephalonica* were provided ad *libitum* (30 per day) on a card and were replaced daily with fresh ones.

To determine the number of host eggs parasitised, the number of black eggs was counted after 2–3 days (Strand 1986) under a dissecting compound microscope (magnification $\times 16$). Upon emergence, the sex ratio (proportion of females in progeny) was also determined. Longevity of adult parasitoids was determined by checking survival of parental females once a day. Trends in survivorship were determined according to Pearl (1928).

Data analysis

Analysis of variance (ANOVA) using the procedure mixed (Proc Mixed, SAS Institute 2000) was used to examine main effects (temperature, relative humidity and strain) and their interactions on parasitism, progeny production, sex ratio as well as adult longevity. To stabilise the variance, the data on numbers of eggs parasitised and adults emerged were log $(x+1)$ transformed before being subjected to analysis (Sokal & Rohlf 1981). When ANOVAs were significant, means were separated using the lsmeans statement with the Tukey option at $P=0.05$ (Zar 1996). A correlation analysis was used to examine the relationship between adult longevity and parasitism for the different strains.

Results

Parasitism

The interactions of temperature, relative humidity and strain affected the number of eggs parasitised (Table II). At 70–80% RH, differences in number of eggs parasitised were observed between strains at all temperatures, except at 30°C (Table III). At 10°C, *T.* sp. nr. *mwanzai* (ex. medium altitude) parasitised more eggs than *T. bruni* (ex. high altitude). At 15°C, *T.* sp. nr. *mwanzai* (ex. medium altitude), *To.* sp. nr. *lutea* (ex. medium altitude) and *T.* sp. nr. *mwanzai* (ex. low altitude) parasitised more eggs than *To.* sp. nr. *lutea* (ex. high altitude) and *T.* sp. nr. *mwanzai* (ex. low altitude) parasitised more eggs than *To.* sp. nr. *lutea* (ex. low altitude). *Trichogrammatoidea* sp. nr. *lutea* (ex. low altitude) also parasitised more eggs than *To.* sp. nr. *lutea* (ex. high

Table II. Results of analysis of variance (ANOVA) showing effects of temperature, relative humidity and strain on parasitism.

Source	*F*	df	*P*
Temperature	221.7	5, 648	<0.0001
RH	1.2	1, 648	0.28
Strain	36.9	5, 648	<0.0001
Temperature × RH	5.2	5, 648	0.0001
Temperature × Strain	7.2	25, 648	<0.0001
RH × Strain	3.1	5, 648	0.005
Temperature × RH × Strain	3.2	25, 648	<0.0001

Table III. Number of host eggs parasitised by six trichogrammatid strains at six constant temperatures at 70–80% RH.

Temperature (°C)	*To*. sp. nr. *lutea* (ex. low altitude)	*T*. sp. nr. *mwanzai* (ex. low altitude)	*To*. sp. nr. *lutea* (ex. high altitude)	*T. bruni* (ex. high altitude)	*T*. sp. nr. *mwanzai* (ex. medium altitude)	*To*. sp. nr. *lutea* (ex. medium altitude)	*F*	df	*P*
10	0.2±0.1ab C	0.3±0.2ab C	0.4±0.2ab B	0.2±0.1b D	0.8±0.2a D	0.2±0.2ab C	2.51	5, 54	0.03
15	0.8±0.3b C	2.2±0.4a C	0.7±0.4c B	0.9±0.3abc CD	2.2±0.3ab C	2.0±0.4ab C	5.06	5, 54	0.0007
20	2.4±0.6b BC	2.0±0.7b C	5.5±0.6a A	1.2±0.6b BC	4.6±0.7ab B	3.0±0.7ab BC	5.13	5, 54	0.0006
25	9.3±1.1a A	9.4±1.0a B	7.2±1.0a A	2.7±1.0b AB	9.4±1.0a A	10.6±1.0a A	8.19	5, 54	<0.0001
30	12.5±1.8a A	7.5±2.0a B	8.8±1.9a A	5.0±2.0a A	8.6±2.0a A	12.1±1.9a A	2.23	5, 54	0.06
35	4.3±1.1abc B	19.8±1.5e A	0.6±1.2ab B	0a BCD	10.7±1.6d A	8.3±1.6cd AB	17.5	5, 54	<0.0001
F	41.9	41.5	25.1	10	44.4	17			
df	5, 54	5, 54	5, 54	5, 54	5, 54	5, 54			
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).

altitude). At 20°C, *To*. sp. nr. *lutea* (ex. high altitude) parasitised more eggs than *To*. sp. nr. *lutea* (ex. low altitude), *T*. sp. nr. *mwanzai* (ex. low altitude) and *T. bruni* (ex. high altitude), while at 35°C, *T*. sp. nr. *mwanzai* (ex. low altitude) parasitised the highest number of eggs. At the same temperature, *T*. sp. nr. *mwanzai* (ex. medium altitude) parasitised more eggs than *To*. sp. nr. *lutea* (ex. low altitude), *To*. sp. nr. *lutea* (ex. high altitude) and *T. bruni* (ex. high altitude). Also at 35°C, *To.* sp. nr. *lutea* (ex. medium altitude) parasitised more eggs than *To*. sp. nr. *lutea* (ex. high altitude) and *T. bruni* (ex. high altitude).

At 40–50% RH, there were no differences between strains at 10 and 20°C, whereas at 15°C, *T*. sp. nr. *mwanzai* (ex. medium altitude) and *To*. sp. nr. *lutea* (ex. medium altitude) parasitised more eggs than *To*. sp. nr. *lutea* (ex. high altitude) and *T. bruni* (ex. high altitude) (Table IV). At 25°C, *To*. sp. nr. *lutea* (ex. medium altitude) parasitised more eggs than *T. bruni* (ex. high altitude) and at 30°C, *T*. sp. nr. *mwanzai* (ex. medium altitude) parasitised more eggs than *T. bruni* (ex. high altitude). At 35°C, *T*. sp. nr. *mwanzai* (ex. medium altitude) parasitised more eggs than *To*. sp. nr. *lutea* (ex. high altitude) and *T. bruni* (ex. high altitude).

Generally, the number of eggs parasitised by most strains at the two humidity levels increased with increasing temperature to a maximum at 30°C. A general trend in the number of eggs parasitised at the two humidity levels could not be clearly established as it varied with species/strain as well as temperature.

Progeny production

Progeny production was similarly affected by the interaction of temperature, humidity and strain (Table V). In general, progeny production at the two humidity levels increased with increasing temperature, following the same pattern as the number of eggs parasitised with respect to temperature (Figure 1a and b).

Sex ratio

Sex ratio was affected by the interaction of temperature and strain ($F=1.6$; df $=25$, 472; $P=0.03$). Since humidity had no affect on sex ratio ($F=0.4$; df $=5$, 472; $P=0.5$), the data were pooled for subsequent analyses. At 10, 15 and 35°C, the sex ratio did not differ between strains (Figure 2). Differences were observed at 20, 25 and 30°C ($P<0.05$). Across all temperatures, there was no clear relationship between temperature and sex ratio for the majority of the trichogrammatid strains studied (Figure 2).

Adult longevity

The longevity of adult parasitoids was influenced by temperature, relative humidity and strain ($F=138.69$; df $=5$, 648; $P<0.0001$, $F=28.6$; df $=1$, 648; $P<0.0001$ and $F=6.09$; df $=5$, 648; $P<0.0001$, respectively). The interactions of temperature and relative humidity ($F=10.32$; df $=5$, 648; $P<0.0001$), temperature and strain ($F=1.87$; df $=25$, 648; $P=0.0066$) as well as relative humidity and strain ($F=4.68$; df $=5$, 648; $P=0.0003$) were signficant.

At 70–80% RH, differences in longevity were observed between strains at 10 and 15°C (Table VI). *Trichogramma bruni* (ex. high altitude) lived longer than *To*. sp. nr. *lutea* (ex. medium altitude) at 10°C, whereas *T*. sp. nr. *mwanzai* (ex. medium altitude)

Table IV. Number of host eggs parasitised by six trichogrammatid strains at six constant temperatures at 40–50% RH.

Temperature (°C)	*To*. sp. nr. *lutea* (ex. low altitude)	*T*. sp. nr. *mwanzai* (ex. low altitude)	*To*. sp. nr. *lutea* (ex. high altitude)	*T. bruni* (ex. high altitude)	*T*. sp. nr. *mwanzai* (ex. medium altitude)	*To*. sp. nr. *lutea* (ex. medium altitude)	*F*	df	*P*
10	0.2±0.1a D	0.2±0.1a B	0.1±0.1a D	0.0±0.1a C	0.2±0.1a D	0.2±0.1a C	0.4	5, 54	0.86
15	1.4±0.4ab CD	1.8±0.4ab B	1.1±0.4b CD	1.1±0.4b BC	2.7±0.4a C	3.1±0.5a B	3.9	5, 54	0.005
20	4.1±0.6a BC	4.3±0.6a A	3.9±0.6a B	2.7±0.7a AB	3.9±0.6a C	4.5±0.6a B	1.1	5, 54	0.4
25	7.3±1.0ab AB	6.4±0.9ab A	6.3±1.1ab AB	2.9±1.2b AB	6.7±0.9ab B	8.3±1.0a A	2.7	5, 54	0.03
30	9.8±1.3ab A	7.1±1.7ab A	8.5±1.4ab A	5.8±1.7b A	13.4±1.3a A	10.3±1.4 ab	3.3	5, 54	0.01
35	6.7±1.6abc AB	6.0±1.0abc A	4.0±1.2ab BC	0a BC	13.3±0.7c A	6.2±1.4abc AB	4.8	5, 54	0.0007
F	10.7	19.5	15.8	7.8	66	24.6			
df	5, 54	5, 54	5, 54	5, 54	5, 54	5, 54			
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).

Table V. Results of analysis of variance (ANOVA) showing effects of temperature, relative humidity and strain on progeny production.

Source	*F*	df	*P*
Temperature	213.2	5, 648	<0.0001
RH	3.6	1, 648	0.06
Strain	27.0	5, 648	<0.0001
Temperature × RH	6.8	5, 648	<0.0001
Temperature × Strain	7.1	25, 648	<0.0001
RH × Strain	4.1	5, 648	0.001
Temperature × RH × Strain	3.4	25, 648	<0.0001

lived longer than *To*. sp. nr. *lutea* (ex. medium altitude) at 15°C. There were no differences in longevity between strains at 20, 25, 30 and 35°C. Adult longevity also varied between temperatures for the different strains.

At 40–50% RH, adult longevity did not differ between the strains at 10, 15 and 20°C, while differences were observed at 25, 30 and 35°C (Table VII). *Trichogramma* sp. nr. *mwanzai* (ex. low altitude), *T*. sp. nr. *mwanzai* (ex. medium altitude) and *To*.

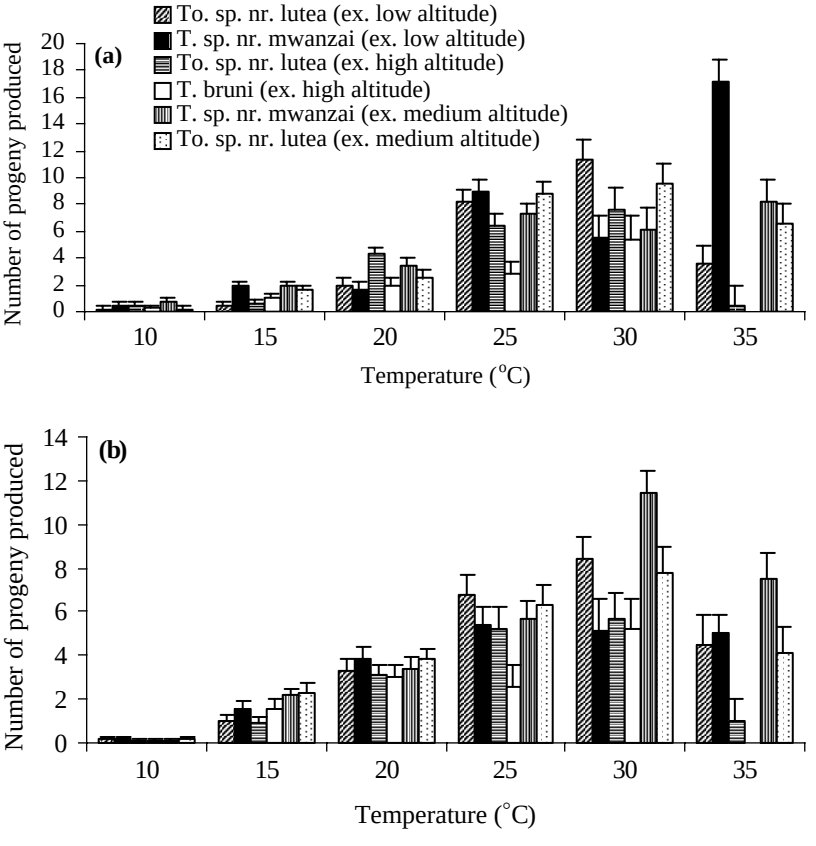

Figure 1. Progeny production by six trichogrammatid species/strains at six temperatures at 70–80% humidity (a) and 40–50% humidity (b).

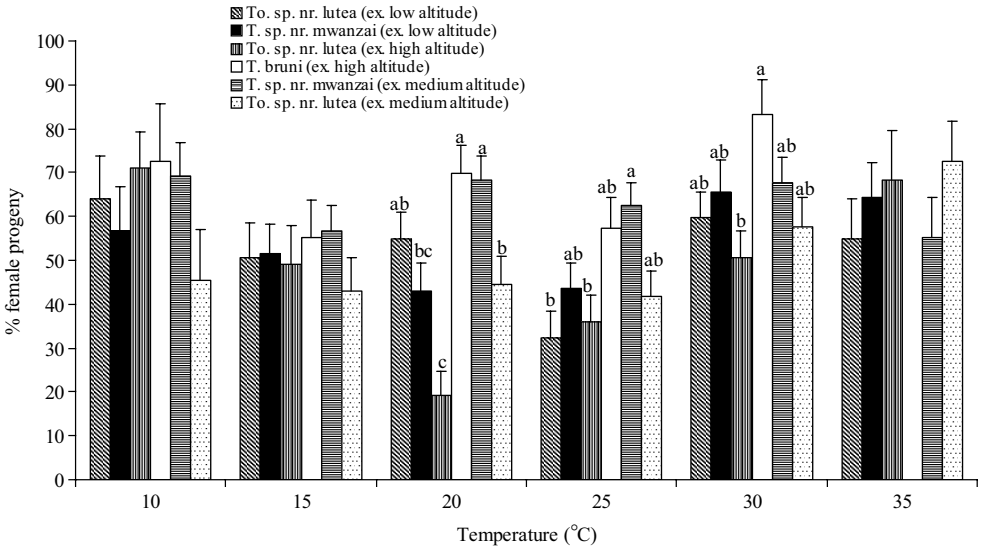

Figure 2. Sex ratio of species/strains at different temperatures. Bars capped with different letters within the same temperature regime are significantly different (Tukey test, $P=0.05$).

sp. nr. *lutea* (ex. medium altitude) lived longer than *T. bruni* (ex. high altitude) at 25°C, while *To*. sp. nr. *lutea* (ex. low altitude) and *T*. sp. nr. *mwanzai* (ex. medium altitude) lived longer than *T*. sp. nr. *mwanzai* (ex. low altitude) and *T. bruni* (ex. high altitude) at 30°C. *Trichogramma* sp. nr. *mwanzai* (ex. low altitude) lived longer than *T. bruni* (ex. high altitude) at 35°C. Adult longevity at 40–50% RH also varied between temperatures for the different strains. Generally, there was an inverse relationship between adult longevity and temperature.

For *To*. sp. nr. *lutea* (ex. low altitude), adult longevity did not differ between the two relative humidity regimes at most temperature regimes but was longer at the lower humidity than higher humidity at 20°C. *Trichogramma* sp. nr. *mwanzai* (ex. low altitude) lived longer at 40–50% RH than at 70–80% RH at 20, 25 and 35°C. *Trichogrammatoidea* sp. nr. *lutea* (ex. high altitude) lived longer at 20 and 30°C at 40–50% RH than at 70–80% RH, whereas *T. bruni* (ex. high altitude) lived longer at 70–80% RH at than at 40–50% RH at 10 and 15°C. *Trichogramma* sp. nr. *mwanzai* (ex. medium altitude) lived longer at 40–50% RH than at 70–80% RH at 20, 25 and 30°C. *Trichogrammatoidea* sp. nr. *lutea* (ex. medium altitude) also lived longer at 40–50% RH than at 70–80% RH at 20 and 25°C.

Longevity of adults was positively correlated with the total number of host eggs parasitised by the various strains ($r=0.26$; $P=0.004$ for *To*. sp. nr. *lutea* (ex. low altitude), $r=0.48$; $P<0.0001$ for *T*. sp. nr. *mwanzai* (ex. low altitude), $r=0.35$; $P<0.0001$ for *To*. sp. nr. *lutea* (ex. high altitude), $r=0.34$; $P=0.0002$ for *T. bruni* (ex. high altitude), $r=0.33$; $P=0.004$ for *T*. sp. nr. *mwanzai* (ex. medium altitude), $r=0.54$; $P<0.004$ for *To*. sp. nr. *lutea* (ex. medium altitude), respectively). The survival of the strains followed a type III survivorship curve at the higher temperatures (30 and 35°C) and a type I survivorship curve at the lower temperatures (Figure 3).

Table VI. Adult longevity (days) of the six trichogrammatid strains at different temperatures at 70–80% RH.

Temperature (°C)	*To*. sp. nr. *lutea* (ex. low altitude)	*T*. sp. nr. *mwanzai* (ex. low altitude)	*To*. sp. nr. *lutea* (ex. high altitude)	*T. bruni* (ex. high altitude)	*T*. sp. nr. *mwanzai* (ex. medium altitude)	*To*. sp. nr. *lutea* (ex. medium altitude)	*F*	df	*P*
10	16.5±3.1ab A	10.6±3ab A	15.1±2.5ab A	17.4±1.3a A	15.5±2.8ab B	8.1±3.0b AB	2.9	5, 54	0.02
15	18.4±4.2ab A	14±2.4ab A	12.8±2.7ab AB	16.5±1.9ab A	25.6±2.4a A	12.7±3.4b A	2.4	5, 54	0.045
20	10±1.9a AB	6.7±2.1a AB	9.6±1.7a AB	9.1±1.4a B	7.8±2.2a C	6.1±1.2a ABC	1.1	5, 54	0.4
25	5.7±1.5a BC	6.7±1.3a ABC	6.5±1.3a BC	6±0.9a B	7.2±1a C	5.8±1.2a ABC	0.3	5, 54	0.9
30	4.2±0.9a BC	2.4±0.3a BC	2.7±0.4a C	2.6±0.4a C	2.4±0.3a CD	3.1±0.5a BC	1.5	5, 54	0.2
35	2.1±0.4a C	1.1±0.1a C	1.8±0.3a C	1.2±0.1a C	1.5±0.3a D	1.4±0.3a C	2	5, 54	0.1
F	9.6	8.9	11.7	45.1	27.2	6.2			
df	5, 54	5, 54	5, 54	5, 54	5, 54	5, 54			
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 $P = 0.05$ (Tukey test).

Table VII. Adult longevity (days) of the six trichogrammatid strains at different temperatures at 40–50% RH.

Temperature (°C)	*To*. sp. nr. *lutea* (ex. low altitude)	*T*. sp. nr. *mwanzai* (ex. low altitude)	*To*. sp. nr. *lutea* (ex. high altitude)	*T. bruni* (ex. high altitude)	*T*. sp. nr. *mwanzai* (ex. medium altitude)	*To*. sp. nr. *lutea* (ex. medium altitude)	*F*	df	*P*
10	13.4±2.9a AB	16.3±2.7a A	16.5±3.4a AB	8.6±1.6a AB	19.3±3.1a A	10.2±2.8a AB	2	5, 54	0.09
15	16.7±3.4a A	15.7±3.7a A	19.2±2.7a A	10.9±1.7a A	19.3±3.7a A	10.9±2.7a AB	1.6	5, 54	0.2
20	18.1±2a A	15.2±2.7a A	22.2±3.1a A	11.3±1.6a A	18.2±2.7a A	17.2±2.7a A	1.5	5, 54	0.2
25	9.2±1.7ab AB	15.1±1.9a A	8.1±2.2ab B	5.4±0.8b BC	13.2±1.7a AB	12.4±2.1ab A	3.9	5, 54	0.004
30	5.9±0.7a BC	2.4±0.3b B	4.4±0.5ab C	2.9±0.5b CD	5.8±0.6a BC	4.2±0.4ab BC	7.4	5, 54	< 0.0001
35	1.5±0.3ab C	2.6±0.3a B	1.8±0.4ab C	1.0b D	1.8±0.3ab C	1.5±0.3ab C	3.8	5, 54	0.005
F	11	12.7	15.1	18.3	15.5	8.8			
df	5, 54	5, 54	5, 54	5, 54	5, 54	5, 54			
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 $P = 0.05$ (Tukey test).

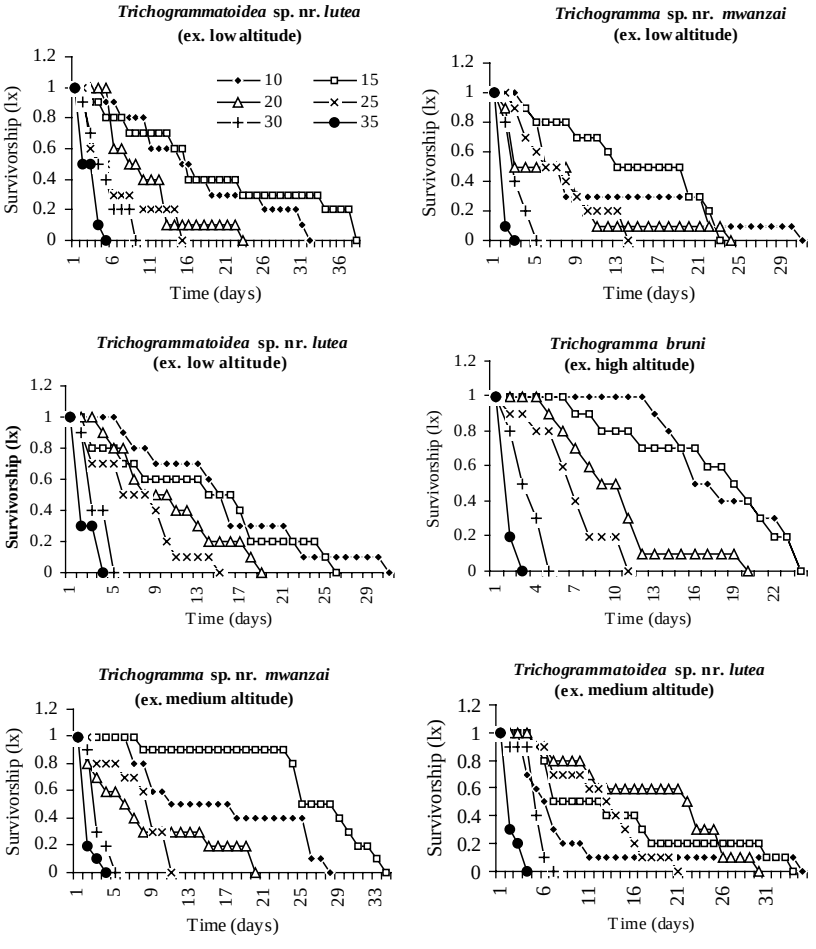

Figure 3. Survivorship curves of six species/strains at six constant temperatures.

Discussion

The effectiveness of released parasitoids to control target pests in biological control programs may be attributed to many factors, but among the most important is the adaptation of a species/strain to climatic conditions (DeBach 1965). Additionally, it is important to determine parasitoid impact on its host in field conditions, which may be affected by biotic and abiotic factors in the agroecosystem. It is possible to identify inherent variations in diversity and select among *Trichogramma* populations for distinct biological responses (Bleicher & Parra 1990). Abraham (1970) observed racial differences in *Trichogramma australicum* Girault and identified strains that were better adapted to warmer temperatures.

In the present study, temperature was the most important factor influencing parasitoid performance. The interaction of temperature and humidity, however, implies that to achieve high efficacy, both temperature and relative humidity need to be considered. Parasitism increased with increasing temperature regardless of the humidity level, although it was low and not different between strains at the lowest temperature (10°C). Parasitism by *T.* sp. nr. *mwanzai* (ex. medium altitude), *T.* sp. nr.

mwanzai (ex. low altitude) and *To*. sp. nr. *lutea* (ex. medium altitude) was higher than the other three species/strains at 15°C, suggesting better performance in cooler environments. These three strains originated from warmer areas but showed better performance at low temperatures than populations from cooler areas, which further suggests that they may be more broadly adapted.

Trichogramma sp. nr. *mwanzai* (ex. medium altitude), *To*. sp. nr. *lutea* (ex. medium altitude) and *T*. sp. nr. *mwanzai* (ex. low altitude) were better suited to performance at high temperatures, hence may perform well in warmer areas. Conversely, *T. bruni* (ex. high altitude) was unable to parasitize at 35°C, suggesting poor performance at warmer temperatures. This strain originated from high altitude where mean monthly temperatures are low (10–23°C) and was apparently not well suited to the high temperature. *Trichogramma* sp. nr. *mwanzai* (ex. low altitude) performed better than other species/strains, which may be related to its history of laboratory rearing. This taxon was reared much longer than the other species/strains, and thus may have been inadvertently selected to perform well under laboratory conditions. However, since all the species/strains were stringently reared continuously as isofemale lines, there was little chance of adaptation to the laboratory environment suggesting that *T*. sp. nr. *mwanzai* (ex. low altitude) may be intrinsically superior.

Progeny production followed a similar trend as parasitism across the different temperature and humidity regimes. Ochiel (1989) observed a significant effect of temperature on progeny production on *T*. sp. nr. *exiguum* when tested at 18 and 30°C. In the present study, *T*. sp. nr. *mwanzai* (ex. low altitude), *T*. sp. nr. *mwanzai* (ex. medium altitude) and *To*. sp. nr. *lutea* (ex. medium altitude), produced higher progeny at the higher temperatures, and thus may be good candidates for deployment in the warmer areas of Kenya. Park et al. (2000) found that emergence of *Trichogramma dendrolimi* was lower at higher (30–32°C) as well as lower temperatures (26°C) and was the highest at 28°C. In the present study, because of the higher parasitism and progeny production, the optimum temperature for the candidate species/strains was around 30°C.

There was no clear relationship between sex ratio and temperature for most species/strains at the two humidity levels. Similarly, Lund (1934) found no consistent relationship between temperature and sex ratio for *Trichogramma minutum*. Ochiel (1989) also reported no significant difference in sex ratio for *T*. sp. nr. *exiguum* with temperature. Harrison et al. (1985), however, reported that temperature affected the sex ratio of *Trichogramma exiguum* and *Trichogramma pretiosum*, with females slightly less abundant at lower and upper developmental temperatures. A similar trend has been reported by Haile et al. (2002) for *Trichogramma* sp. nr. *mwanzai* in Kenya. The present results, however, showed that temperature affected the sex ratio of some strains, but not all.

Generally, there was an inverse relationship between survivorship and temperature. Similarly, Harrison et al. (1985) found that longevity of *T. exiguum* Pinto and Platner and *T. pretiosum* Riley significantly decreased with an increase in temperature (15–30°C). The same trend has also been reported by Yu et al. (1984) for *T. minutum* Riley. The differences observed in longevity between strains within the different temperatures and humidity levels are suggestive of differences in adaptation to environmental conditions. The ability of a parasitoid to perform in a particular agro-ecosystem is a critical factor in evaluating the potential of a parasitoid as a natural

enemy (Tillman & Powell 1991). It is therefore important that the choice of the strain should be made on the basis of the climatic conditions of the area of release. There was no clear relationship between source (altitude and climate) and the performance of the strains at the different temperatures in the present study.

Different researchers have used different biological attributes in evaluating *Trichogramma* performance. Hirashima et al. (1990) used adult longevity to compare the potential of two *Trichogramma* species in which *Trichogramma chilonis* Ishii was superior (5 days) compared to *Trichogramma ostriniae* Pang and Chen (4.6 days). Hassan and Guo (1991) selected appropriate *Trichogramma* species to control the European corn borer, *Ostrinia nubilalis* Hubner, on the basis of their fertility. It is, however, essential that longevity be matched by greater fecundity, if a generational response is desired. The two attributes were found in *T.* sp. nr. *mwanzai* (ex. low altitude), *T.* sp. nr. *mwanzai* (ex. medium altitude) and *To.* sp. nr. *lutea* (ex. medium altitude) in the present study. The existence of a positive correlation between fecundity and adult longevity by the species/strains suggests good performance. Because *H. armigera* and *C. cephalonica* are equally suitable (Muholo 2002), the three strains are potentially useful for control of *H. armigera*. Bourchier and Smith (1996) and Dutton et al. (1996) also used fecundity on a factitious host to predict field parasitism.

In conclusion, three strains; *T.* sp. nr. *mwanzai* (ex. low altitude), *T.* sp. nr. *mwanzai* (ex. medium altitude) and *To.* sp. nr. *lutea* (ex. medium altitude) appeared to be the most promising candidates for use in augmentative biocontrol program against *H. armigera* in warmer areas where the pest is a serious problem.

Laboratory studies at different temperatures provide useful information on the performance of potential insects (Wang et al. 1997). They also indicate the potential effectiveness of parasitoids in the field (Force & Messenger 1964). However, according to Omer et al. (1996), it is important that verifications are made in the field where conditions are variable.

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