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Influence of temperature on the development, reproduction and longevity of *Ceratothripoides claratris* (Thysanoptera: Thripidae) on tomatoes

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Abstract

Ceratothripoides claratris (Shumsher) is a serious pest attacking tomatoes in Thailand. Temperature-dependent development of *C. claratris* was studied at seven constant temperatures, i.e. 22, 25, 27, 30, 34, 35 and 40°C. Pre-adult survivorship was greatest (95%) at 25 and 30°C and shortest at 22°C. Egg-to-adult time decreased within the range of 20 to 30°C and at 34°C it started to increase. The lower thermal threshold for egg-to-adult development was estimated at 16 and 18°C by linear regression and the modified Logan model, respectively. The optimum temperature for egg-to-adult development was estimated at 32–33°C by the modified Logan model. The influence of temperature on reproduction and longevity of *C. claratris* was determined at 25, 30 and 35 and 40°C. Both inseminated and virgin females failed to reproduce at 40°C. Virgin females produced only male offspring, confirming arrhenotoky. The sex ratio of the offspring of fertilized females was strongly female-biased, except at 25°C. Mean total fecundity per female and mean daily total fecundity per female were highest for both virgin and inseminated females at 30°C. Female longevity was longest at 25°C and shortest at 40°C. Male longevity was longest at 30°C and shortest at 40°C. The net reproductive rate (R_0) and intrinsic rate of natural increase (r_m) was greatest at 30°C while, mean generation time (G) and the doubling time (t) were highest at 25°C. The finite rate of increase (λ) was fairly constant (1.1–1.5 days) over the three temperatures tested. The pest potential of *C. claratris* for tropical Asia is discussed.

Introduction

Ceratothripoides claratris (Shumsher) (Thysanoptera: Thripidae), previously described as *Taeniothrips claratris* Shumsher and *Mycterothrips moultoni* Seshadri & Ananthakrishnan, was first detected in northern Thailand in 1987 attacking melons, *Cucumis melo* L. (Cucurbitaceae), (Okajima *et al*., 1992). It was subsequently found on egg plants, *Solanum melongena* L. (Solanaceae) in the same region (Jangvitaya, 1993). Mound & Kibby (1998) also recorded *C. claratris* infestations of cucurbits in Thailand at about the same time. *Ceratothripoides claratris* was first detected on tomatoes in Thailand in 1999 (Murai *et al*., 2000). Murai *et al.* (2000) reported that no other thrips species were found on tomatoes in central Thailand. In addition to *C. claratris*, *Thrips palmi* Karny (Thysanoptera: Thripidae) also occurs in

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fields and greenhouses in the greater Bangkok area, though in very low numbers. *Ceratothripoides claratris* has also been found infesting tomatoes in Malaysia in 1999 (S. Okajima, cited in Murai *et al.*, 2000). Jangvitaya (1993) reported *Luffa acutangula* L. (Cucurbitaceae) and *Clitoria ternatea* L. (Fabaceae) as additional host plants of *C. claratris* in Thailand. In a host plant preference study, *C. claratris* heavily attacked and successfully reproduced on cucumber, pumpkin, cowpea, yard long bean and chili (D. Premachandra, unpublished data). Moreover, *C. claratris* is apparently vectoring tomato necrotic spot virus (TNSV) on tomatoes (D. Premachandra, unpublished data).

Rodmui (2002) studied the life cycle of *C. claratris*. As in other thrips species, *C. claratris* has six development stages, i.e. the egg, which is embedded in the plant tissue, two active larval instars, two inactive pupal instars, i.e. prepupa and pupa, and the adult. Adults and the two larval instars feed on the foliage. The late second instar larvae drop off the plants and pupate in the soil or on leaf litter. Adults are dark brown in colour and females have an average width of about 0.20 mm and a length of 0.98 mm, whereas males are slightly smaller (Rodmui, 2002).

Under greenhouse and field conditions in Thailand *C. claratris* preferentially attacks leaves of tomato, and to a lesser extent stems and fruits (Murai *et al.*, 2000; Rodmui, 2002). The damaged leaves initially appear bleached and finally dry out. Under severe infestations in greenhouses, tomato plants die seven weeks after initial infestation, i.e. prior to first fruit setting. Hence, *C. claratris* can cause a total loss of greenhouse tomatoes in Thailand.

Although *C. claratris* is an important vegetable pest in Thailand, to date only one study has addressed its biology and reproduction (Rodmui, 2002). However, at present no information on the impact of temperature on the development, reproduction and survivorship of *C. claratris* is available. In-depth life cycle studies are essential for developing integrated pest management strategies, e.g. for determining the accurate timing for releases of natural enemies and/or application of selective insecticides. Temperature-dependent developmental rates of an insect are important to explain and predict the fluctuations in population densities. Moreover, parameters generated from life-fertility studies are crucial components for a better understanding of the population dynamics of a species (Southwood, 1978). This study is part of a larger project that seeks to develop sustainable vegetable production systems under protected cultivation in the humid tropics, where temperatures in greenhouses are of paramount importance for plant growth, as well as for incidence of, and damage caused by pests and diseases. Hence, the objectives of this study were to investigate the temperature-dependent development, reproduction and longevity of *C. claratris*.

Materials and methods

Thrips source and the host plant

Adult *C. claratris* were initially collected from tomato plots at the Asian Institute of Technology (AIT), Bangkok, Thailand. Thereafter, thrips were reared on potted tomato plants *Lycopersicon esculentum* Mill. (Solanaceae), cv. King Kong II in a small net-house (10 × 20 m, mesh size of the net approximately 400 µm). *Ceratothripoides claratris* was identified based on its morphological characteristics, and voucher specimens were deposited at the Division of Entomology, Department of Agriculture, Bangkok, Thailand and the Senckenberg Museum, Frankfurt, Germany. All experiments were carried out on tomato plants (cv. King Kong II).

Experimental conditions

The development of *C. claratris* was studied in a temperature-controlled climate chamber at 22, 25, 27, 30, 34, 35 and 40 ± 1°C, 75 ± 5% relative humidity (rh) and a 12L:12D photoperiod. Experiments on reproduction and longevity of the thrips were conducted at 25, 30 and 35 and 40 ± 1°C, 75 ± 5% RH and a 12L:12D photoperiod.

Development

Cohorts of similarly-aged eggs were obtained by allowing groups of adult females of *C. claratris* (approximately 250 individuals) to oviposit on excised tomato leaflets for 4 h at the desired temperature. Leaflets were kept in a Petri dish (8.5 × 1.5 cm) lined with a thin layer (approximately 1.5 cm thickness) of a mixture of plaster of Paris and charcoal (ratio 9:1). In order to keep the leaflets viable, petioles were wrapped in wet cotton. Two holes (2 cm diameter, covered with a 64 µm mesh nylon tissue) were cut into the lid of the Petri dish to facilitate ventilation. After introducing the adults for oviposition, the Petri dish was thoroughly sealed, using modelling clay, to prevent thrips from escaping. After 4 h, the adults were removed from the leaflet with a fine camel hair brush, and the eggs incubated. In preliminary experiments at 40°C, excised tomato leaflets started to deteriorate after one day. Hence, at 40°C, instead of leaflets, a whole tomato plant was used to obtain eggs and for subsequent rearing of the thrips larvae.

For the experiments, leaf discs (2 cm diameter) were punched out from fully grown tomato leaflets. The discs were placed abaxial surface uppermost on water agar (0.9%, 1.5 cm thickness) in a small plastic container (5 × 4 × 3 cm), henceforth referred to as a 'larval container'. One hole (1 cm diameter, covered with a 64 µm mesh nylon tissue) was cut into the centre of the lid. An individual newly emerged first instar larva was placed on a leaf disc with a fine camel hair brush. Every two days, the larvae were transferred to fresh leaf discs. The second larval instar was determined by the occurrence of exuviae. In preliminary experiments late second instar larvae started to leave the leaf discs for pupation. Hence, 12 h after moulting the second instar larvae were transferred to a separate 'pupal container' and reared there until emergence of the adults. Pupal containers were identical to larval containers except that the base was lined with a mixture of plaster of Paris and charcoal (9:1). To facilitate pupation, the leaf disc with the second instar larva was sandwiched between two fresh leaf discs. Subsequently, the space between the lid and the pupal container was sealed with modelling clay. Development duration and survival of immature stages, i.e. egg, first instar larva, second instar larva, prepupa and pupa, were determined at 12 h intervals under a stereo microscope. At least 30 individual larvae were observed at each temperature tested. The sex of the emerged adults was determined and the development time of males and females were calculated separately. The data on the developmental time were used to establish the basic thermal requirements of the different life stages of *C. claratris*.

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Reproduction and longevity

Reproduction was quantified both for inseminated and virgin females. To obtain synchronized-aged females, second instar larvae from the rearing unit were kept on tomato leaves in a Petri dish (8.5 × 1.5 cm) until they reached the pupal stage. Female pupae were then identified and kept separately for generating virgin females. For studies with inseminated females, a virgin female and a male were simultaneously introduced into the assay arena, and after 24 h the male was removed. In these experiments, excised tomato leaflets with petioles were used instead of leaf discs. The petiole was inserted into a small glass vial (1.4 × 1.5 × 4.4 cm) filled with water agar (0.9%). The vial was placed in a plastic container (7.5 × 5.5 × 7 cm), and the base of the vial (approx. 1 cm in depth) was embedded in a layer of plaster of Paris and charcoal (9:1 ratio, 3 cm thickness). One hole (1 cm diameter, covered with a 64 µm mesh nylon tissue) was cut into the centre of the lid. For a precise determination of the pre-oviposition period, females were transferred to fresh tomato leaflets every 6 h until day 3 of the experiment. Thereafter, tomato leaflets were replaced every 24 h until the death of the females. Leaflets bearing eggs were incubated at the appropriate temperature. Fecundity estimates, i.e. total and daily fecundity, were based on the number of emerged first instar larvae on the leaflets. At least 100 first instar larvae produced by virgin and inseminated females were randomly selected and individually reared to adulthood for sex determination at each temperature regime tested. In addition, survival of virgin and inseminated females was recorded daily. Longevity of male *C. claratris* was studied in assay arenas similar to the ones used for females. Newly emerged males were individually placed on a single tomato leaflet in a plastic container. Every three days males were transferred to a fresh tomato leaflet, and survival was recorded daily. Data on pre-adult survival, daily fecundity of individual, inseminated females and the sex ratio of their offspring at each temperature tested, was used to construct the lifetime-fertility tables.

Data analyses

Data on development time of the different life stages and egg-to-adult time, adult longevity and fecundity of virgin and inseminated females were compared across temperatures using analysis of variance (ANOVA) (GLM procedure; SAS Institute (1999)). In cases of significance, means were separated using LSD ($P = 0.05$). For estimation of the lower developmental threshold (To = intercept/slope) and the thermal constant (K = 1/slope = the number of day-degrees to complete the pre-reproductive phase; Campbell *et al*., 1974), a simple regression over the linear range, of the relationship between temperature (T) and developmental rates was used (Campbell *et al*., 1974). The modified Logan model (Logan *et al*., 1976) by Lactin *et al*. (1995)

$$R(T) = e^{\rho T} - e^{[\rho Tmax - (Tmax - T)/\Delta]} + \lambda$$

where T is the temperature in degrees Celsius (°C), ρ, Tmax, Δ and λ are fitted coefficients, was used to describe temperature-dependent development rates of adult *C. claratris*.

The life-fertility table parameter estimates, i.e. the intrinsic rate of increase (r_m), net reproductive rate (R_0), mean generation time (G), doubling time (t) and the finite rate of increase (λ), were calculated using the jackknife program (Hulting *et al*., 1990). Differences in these estimates over the temperatures tested were compared using the Newman-Keuls sequential test (Sokal & Rohlf, 1995) on the basis of jackknife estimates of variance (Meyer *et al*., 1986).

Results

Development

All life stages, i.e. the first instar larva, second instar larva, prepupa, pupa and adults of *C. claratris* developed at the temperatures tested except at 40°C when the eggs did not hatch (table 1). At 25 and 30°C, pre-adult survivorship was 95%. At 27, 34 and 35°C pre-adult survivorship ranged from 72–90%, and the lowest survivorship (43%) was recorded at 22°C. Egg-to-adult time differed significantly across temperatures ($F = 858$; d.f. = 5, 291; $P < 0.0001$) with the longest and shortest duration at 22 and 30°C, respectively. Egg-to-adult developmental time decreased within a range of 22–30°C; thereafter it started to increase (table 1). Total developmental time of males and females did not differ significantly at the six temperatures tested. However, the development time of the immature stages of *C.*

Table 1. Mean (± SE) developmental time (in days) of different life stages of *Ceratothripoides claratris* at seven constant temperatures.

Life stages	Temperatures (°C)						
	22	25	27	30	34	35	40
Eggs	6.64 ± 0.04 a[1] (67)[2]	4.20 ± 0.04 b (97)	4.12 ± 0.09 b (60)	3.07 ± 0.02 c (74)	2.61 ± 0.03e (59)	2.81 ± 0.05 d (86)	Did not hatch
Larva I	3.16 ± 0.04 a (67)	2.57 ± 0.03 b (97)	2.05 ± 0.04 c (60)	2.01 ± 0.01 c (74)	2.00 ± 0.00 c (59)	1.98 ± 0.01 c (86)	–
Larva II	4.32 ± 0.11 a (67)	3.74 ± 0.05 b (97)	1.63 ± 0.21 d (56)	1.15 ± 0.07 e (73)	2.23 ± 0.08 c (59)	2.28 ± 0.08 c (78)	–
Prepupa	1.75 ± 0.06 a (34)	0.78 ± 0.03 b (93)	0.77 ± 0.05 b (55)	0.78 ± 0.04 b (70)	0.80 ± 0.04 b (52)	0.77± 0.04 b (70)	–
Pupa	3.82 ± 0.20 a (32)	3.27 ± 0.05 b (92)	2.76 ± 0.09 c (54)	1.79 ± 0.04 d (70)	1.71 ± 0.08 d (48)	1.88 ± 0.05 d (64)	–
Egg to adult	19.55 ± 0.31 a (29)	14.55 ± 0.07 b (92)	11.37 ± 0.18 c (54)	8.80 ± 0.09 e (70)	9.42 ± 0.10 d (48)	9.76 ± 0.08 d (62)	–

[1] Means followed by the same letter within rows are not significantly different ($P = 0.05$, LSD multiple range test (SAS Institute, 1999));
[2] numbers entering each life stage.

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Table 2. Estimates of the linear regression analyses and lower thermal thresholds and the thermal constants for egg, second instar larvae, pupae and egg-adult stages of *Ceratothripoides claratris*.

Life stages	Linear range (°C)	Regression equations [a]	R^2	F values	*P*>F	T_0 [b]	K [c]
Egg	22–34	Y = –0.2571 + 0.0192X	0.91	3021	0.0001	13.36	51.90
Larva II	22–30	Y = –2.922 + 0.1345X	0.43	172.2	0.0001	21.70	7.44
Pupa	22–34	Y = –0.4997 + 0.0340X	0.53	275.8	0.0001	14.70	29.41
Egg – adult	22–30	Y = –0.1354 + 0.0083X	0.91	2078	0.0001	16.37	120.92

[a] Calculated after Campbell *et al*. (1974), where X is the temperature (°C) and Y is the developmental rate (1/developmental time).
[b] Lower development threshold (°C).
[c] Thermal constant (in day degrees).

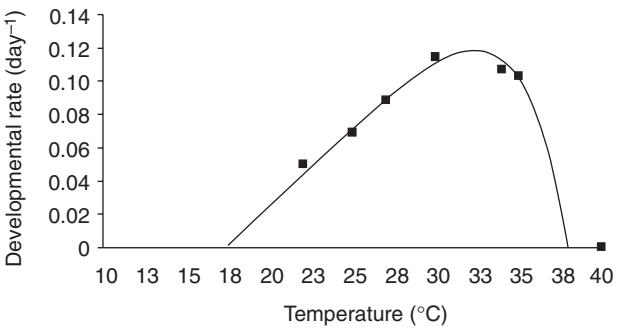

Fig. 1. Developmental rate of *Ceratothripoides claratris* expressed as a temperature (°C) function using the modified Logan model.

claratris was significantly influenced by the temperatures tested (table 1). Duration of egg, larval and pupal stages was significantly longer at 22°C than at all other temperatures tested (eggs, F = 1258; d.f. = 5, 364; $P < 0.0001$; first instar larva, F = 301.0; d.f. = 5, 356; $P < 0.0001$; second instar larva, F = 216.3; d.f. = 5, 320; $P = 0.0001$; prepupa, F = 69.4; d.f. = 5, 307; $P < 0.0001$; pupa, F = 126.9; d.f. = 5, 292; $P < 0.0001$). No significant differences in development time of first instar larva and prepupa and pupa were recorded above 25 and 27°C, respectively (table 1). In terms of total development time, the egg stage lasted longest (range 28–36%) and the prepupal stage shortest (range 5–9%) at all temperatures.

For all life stages of *C. claratris* significant relationships between the development rate and the temperatures tested were recorded (table 2). For egg and egg-to-adult time the relationships between development rates and temperatures were strongly linear ($R^2 = 0.91$, $P < 0.0001$) at 22–34°C and 22–30°C, respectively, while weaker relationships were recorded for the second instar larva (22–35°C) and pupa (22–34°C). Linear regressions did not yield a good fit for development of the first instar larva and prepupa. The modified Logan model provided a good fit for data on egg-to-adult time within a range of 22–35°C ($R^2 = 0.90$, $P < 0.0001$) (fig. 1). The fitted parameters were estimated as $\rho = 0.00813$, $T_{max} = 43.5$, $\Delta = 2.921$ and $\lambda = 21.151$. Based on this model, the lower, optimum and maximum temperatures were estimated as 18, 32–33 and 38°C, respectively.

Reproduction and longevity

Both inseminated and virgin females failed to reproduce at 40°C. At 25°C, the pre-oviposition period was significantly longer for both inseminated (F = 26.84; d.f. = 2, 36; $P < 0.0001$) and virgin females (F = 18.28; d.f. = 2, 34; $P < 0.0001$) than at the other two temperatures tested (table 3). Except at 35°C, duration of pre-oviposition varied significantly between inseminated and virgin females. At 25 ($P < 0.004$, t test) and 30°C ($P < 0.0001$, t test), the pre-oviposition period of inseminated females was longer than that of virgin females.

Mean total fecundity per female and mean daily total fecundity per female were significantly higher for both virgin (for mean total fecundity per female F = 4.36; d.f. = 2, 44; $P < 0.0187$; for mean daily total fecundity per female F = 31.4; d.f. = 2, 44; $P < 0.0001$) and inseminated females (for mean total fecundity per female F = 14.03; d.f. = 2, 43; $P < 0.0001$; for mean daily total fecundity per female F = 34.15; d.f. = 2, 43; $P < 0.0001$) at 30°C than at the other two temperatures tested (table 3). Mean total fecundity of inseminated and virgin females did not differ at 25 and 30°C.

Mean longevity of inseminated females and males of *C. claratris* differed significantly among the three temperatures tested. Female longevity was significantly longer at 25°C (F = 26.84; d.f. = 3, 109; $P < 0.0001$) than at the other three temperatures. Male longevity was longest at 30°C, and shortest for both females and males at 40°C. No significant differences in longevity of male and female thrips were found at 25 and 35°C. In contrast, at 30°C, male longevity was significantly longer than that of females ($P < 0.0005$, t test), while at 40°C female longevity was significantly longer than that of males ($P < 0.0001$, t test).

Virgin females produced only male offspring, whereas inseminated females had both male and female offspring. The F1 sex ratio of mated females was strongly female biased at 30 and 35°C with 71% and 65% female progeny, respectively. In contrast, at 25°C, the F1 of inseminated females was male biased, with a mean proportion of 62% males (table 3).

The pattern of reproduction and survivorship of inseminated and virgin females at three temperatures are shown in fig. 2. Survivorship, as well as progeny production declined as females aged at each temperature tested. Post-oviposition periods were short (1–3 days) for inseminated and virgin females across the temperatures tested. For both types of females, the pattern of oviposition was erratic at 25°C (fig. 2 a,b). In contrast, an ovipositional peak was evident at 6 (fig. 2c) and 4 days (fig. 2e) after emergence in inseminated females at 30°C and in both inseminated and virgin females at 35°C (fig. 2e,f), respectively. Moreover, at 30°C, peaks in oviposition occurred in virgin females at 7 and 9 days after emergence (fig. 2d).

Life-history parameters of inseminated thrips females

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Table 3. Mean (± SE) pre-oviposition period (days), total fecundity, daily fecundity per female, sex ratio and longevity of inseminated females and males (days) of *Ceratothripoides claratris* at different constant temperatures.

Parameters	Temperatures (°C)			
	25	30	35	40
Pre-oviposition period of virgin females	2.5 ± 0.17 a	1.38 ± 0.04 c	1.82 ± 0.01 b	–
Pre-oviposition period of inseminated females	3.3 ± 0.19 a	1.75 ± 0.06 b	1.76 ± 0.14 b	–
Total fecundity of virgin females	69.8 ± 13.95 b	110.07 ± 11.16 a	62.71 ± 11.33 b	–
Total fecundity of inseminated females	44.9 ± 6.53 c	116.50 ± 11.65 a	70.06 ± 9.78 b	–
Daily fecundity per virgin female	3.17 ± 0.41 a	9.22 ± 0.80 b	6.08 ± 0.66 c	–
Daily fecundity per inseminated female	2.37 ± 0.39 a	10.30 ± 1.54 b	5.39 ± 0.55 c	–
Sex ratio (% female progeny)	38 ± 5.72 b	71 ± 7.72 a	65 ± 5.90 a	–
Female longevity	18.5 ± 1.51 a	12.2 ± 0.73 b	10.9 ±0.90 b	2.79 ± 0.25 c
Male longevity	14.1 ± 2.12 ab	17.1 ± 1.14 a	11.0 ± 1.54 b	1.21 ± 0.20 c

–, No progeny production. Within rows, means followed by the same letter are not significantly different ($P = 0.05$, LSD multiple range test).

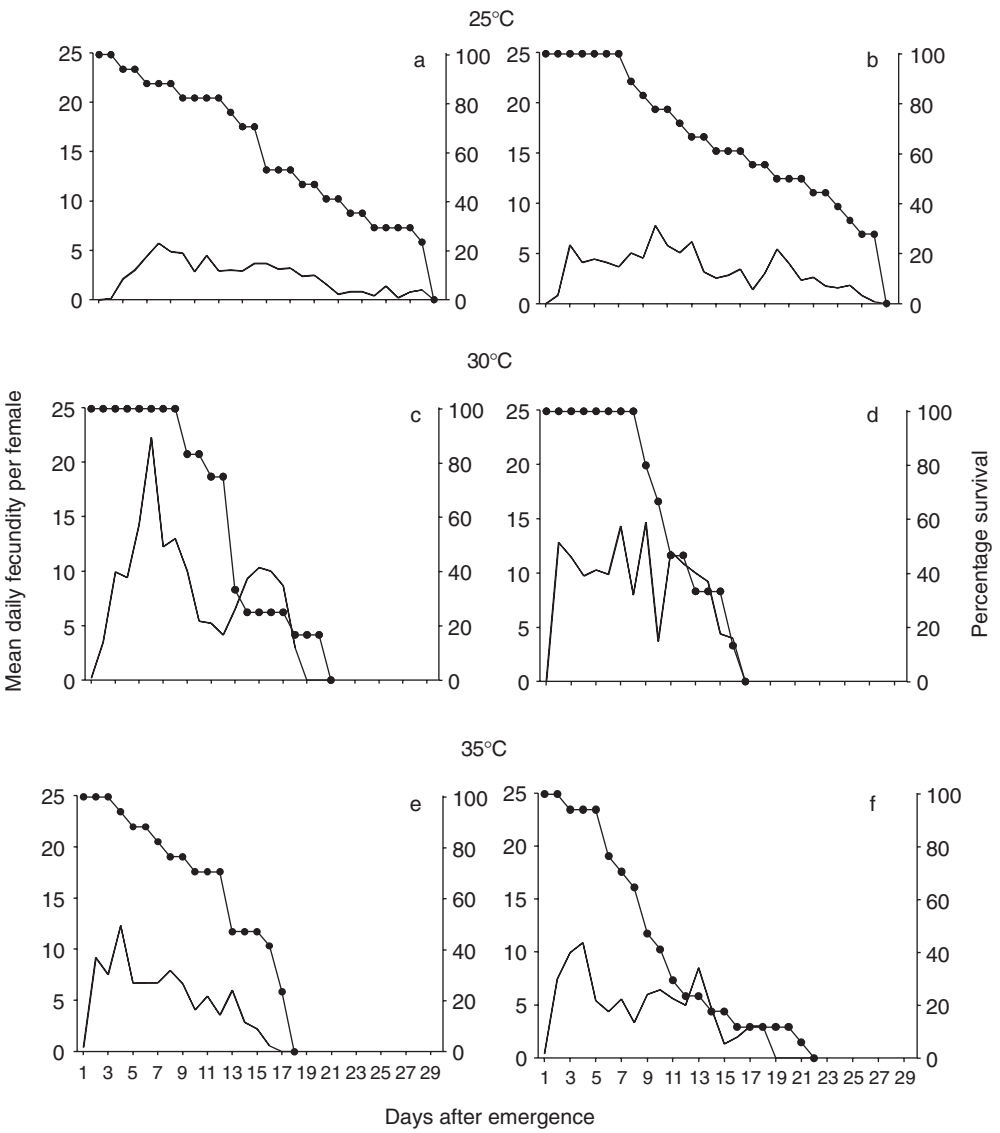

Fig. 2. Age-specific reproduction (——) and survivorship (–●–) of inseminated and virgin females of *Ceratothripoides claratris* at 25, 30 and 35°C. (a) inseminated, 25°C; (b) virgin, 25°C; (c) inseminated, 30°C; (d) virgin, 30°C; (e) inseminated, 35°C; (f) virgin, 35°C.

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varied significantly with temperatures (table 4). The net reproductive rate (R_0) was significantly greatest at 30°C; it was twice as high as at 35°C and five times higher than at 25°C. The intrinsic rate of natural increase (r_m) was significantly highest and lowest at 30 and 25°C, respectively. With 20.67 and 5 days the maximum mean generation time (G) and the doubling time (t), respectively, were recorded at 25°C. The finite rate of increase (λ) remained fairly constant over the three temperatures tested.

Discussion

Temperature is a key factor for the development, survival and reproduction of poikilothermic organisms (Andrewartha & Birch, 1954; Sharpe & DeMichele, 1977). Information on temperature-dependent development, survivorship and reproduction of different insects, including thrips (Kawai, 1985; Shibao, 1996; Murai, 2001; Hoddle, 2002) is well documented. This is the first report on development, reproduction and longevity of *C. claratris* at different constant temperatures. Temperature had a profound effect on the development, fecundity and longevity of *C. claratris*. At 22°C, development of all thrips life stages was considerably prolonged and the pre-imaginal mortality was highest (57%). At 40°C, development of *C. claratris* eggs was inhibited. Estimates of the modified Logan model indicate 38°C as the maximum temperature for development of *C. claratris*. Best performance of *C. claratris* was recorded at 30°C, as shown by the high level of pre-adult survivorship, coupled with the respective estimates of the different life-history parameters, i.e. the higher net reproductive rate (R_0), intrinsic rate of increase (r_m) and shorter mean generation time (G) and doubling time (t). Moreover, estimates of the modified Logan indicate values of an optimum temperature for the development of *C. claratris* at 32–33°C.

Inhibition of egg development at the highest temperature tested (i.e. 40°C) was most likely due to desiccation under heat stress. Low or no mortality was recorded for the first instar larva at all temperatures. Possibly emerging young larvae still sustained some nutritive reserves from the egg stage. In a life table study with *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae), however, Hoddle (2002) reported highest mortality in first instar larva at the lowest temperature (i.e. 15°C) tested. A possible reason for this discrepancy might be the fact that *S. perseae* is more a thrips of sub-tropical to temperate climates, whereas *C. claratris* is obviously a species well adapted to tropical conditions. In our experiments, high mortality of second instar larvae (87%) occurred at the lowest temperature (22°C), indicating that second instar larvae are the most susceptible pre-imaginal life stage of *C. claratris* to low temperatures. Considerably lower mortalities at all temperatures tested were recorded in the pupal stages. In general, temperature greatly affected the development time of *C. claratris* larvae. For instance, at 22°C compared to 30°C, a four times longer developmental time was recorded in second instar larvae. According to Trichilo & Leigh (1988), factors like temperature that delay the development times will act primarily on the active moving larvae, possibly through a reduced food intake (Bakker, 1961). In the present study, temperature had little to no effect on the development time of prepupae and pupae.

Table 4. Mean (± SE) population growth parameters of *Ceratothripoides claratris* at three constant temperatures.

Parameters	Temperatures (°C)		
	25	30	35
r_m	0.139 ± 0.007 c	0.347 ± 0.010 a	0.281 ± 0.010 b
R_0	17.60 ± 2.682 c	84.39 ± 8.450 a	38.45 ± 5.390 b
G	20.67	12.80	13.00
λ	1.15	1.41	1.32
t	5.00	2.00	2.47

Means followed by the same letter within rows are not significantly different (P = 0.05, Student-Newman-Keuls sequential test). r_m, intrinsic rate of natural increase; R_0, net reproductive rate; G, mean generation time (days); λ, finite rate of increase; t, doubling time (days).

Rodmui (2002) reported a slightly shorter egg-to-adult time of *C. claratris* at 25°C than in this study, possibly due to differences in methodology. More data on the effect of temperature on development are available for several important thrips pests in the tropics and subtropics, such as *T. palmi*, *Scirtothrips dorsalis* Hood, *Thrips tabaci* Lindeman and *Thrips hawaiiensis* (Morgan) (all Thysanoptera: Thripidae). For instance, temperatures exceeding 30°C have detrimental effects on the egg development in *T. hawaiiensis* (Murai, 2001). Similar effects have been reported in *T. tabaci*, *Frankliniella intonsa* (Trybon) and *Frankliniella occidentalis* (Pergande) (all Thysanoptera: Thripidae) (Murai, 1988, 2000; Katayama, 1997), corroborating results of this study. Under laboratory conditions on cucumbers, the lower threshold temperature for development of *T. palmi* was estimated at 11.6°C (Kawai, 1985) which is markedly lower than that of *C. claratris*, indicating that *C. claratris* has a greater potential for development at higher temperatures than *T. palmi*. Likewise, *T. hawaiiensis*, *T. tabaci* and *S. dorsalis* have lower threshold temperatures for development from egg to adult (Tatara, 1994; Murai, 2000, 2001) than *C. claratris*. Thus, it appears that *C. claratris* in comparison to other important thrips pests in the tropics and subtropics is less tolerant to cooler but better adapted to higher temperatures.

Reduced longevity of both males and females and the inhibition of progeny production by both inseminated and virgin females at 40°C emphasize the adverse effects of high temperatures on reproduction and longevity in *C. claratris*. At 25°C, even though females lived longer, they were less fecund. The significantly lower longevity of females compared to males at 30°C was most likely associated with the increased reproductive capacity of the females at this temperature (Gaum *et al.*, 1994). *Ceratothripoides claratris* reproduces by arrhenotokous parthenogenesis. Except at 25°C, the sex ratios of inseminated females were strongly female-biased, leading to a rapid increase in thrips density. The male-biased sex ratio at 25°C can possibly be explained by fewer matings, sperm depletion and reduced sperm viability. In addition, at 25°C females lived longer than at the other temperatures tested. In western flower thrips and in *Spalangia cameroni* Perkins (Hymenoptera: Pteromalidae) the proportion of daughters in the progeny decreased with age, presumably as a result of sperm depletion (Higgins *et al.*, 1992; King, 2000). The high net reproductive rate at 30°C resulted from a significantly higher fecundity compared to the other temperatures tested and a high proportion of females in the F1. The pronounced ovipositional peaks during the early reproductive cycle at higher temperatures

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are possibly associated with a higher metabolic rate (Sharpe & DeMichele, 1977). The small r_m value at 25°C mainly resulted from the reduced fecundity of inseminated females at lower temperatures. In addition, the doubling time and mean generation time were also longer at 25°C, contributing to a lower r_m value. The life-history estimates of *C. claratris* at 25°C reported by Rodmui (2002) correspond well with our data, except for the net reproductive rate which was two times higher in the previous study. Once again, methodological differences and the different models used for the analysis of life-history parameter estimates may account for this difference. The net reproductive rate (R_0) of *T. palmi*, *T. hawaiiensis* and *T. tabaci* at 25°C are higher than that of *C. claratris*. In contrast, at 30 and 35°C the net reproductive rate of *C. claratris* is four and two times higher than that of *T. palmi*, respectively. Likewise, at 30°C the intrinsic rate of increase of *C. claratris* is three times higher than that of *T. palmi* (Kawai, 1985).

The data on development, reproduction and longevity of *C. claratris* indicate that this species is better adapted to high temperatures (i.e. 30–35°C) than other important tropical thrips species like *T. palmi* and *S. dorsalis*. Moreover, the relatively short life cycle of *C. claratris*, coupled with its high reproductive potential, female biased sex ratio and long lifespan can lead to a rapid population build up, both in the field and under greenhouse conditions in the tropics. At present, little is known on the host plant spectrum and the geographic distribution of *C. claratris*. However, our results clearly show that *C. claratris* has the potential to become a serious constraint for tomato production in tropical Asia. In ongoing studies we are investigating the host plant preference of and virus transmissibility by *C. claratris*.

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Identification, Biology and Control

Zhi-Qiang Zhang, Landcare Research, Auckland, New Zealand, the Natural History Museum, London, UK, and Fudan University, China

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