BioControl (2009) 54:743–750
DOI 10.1007/s10526-009-9225-x

Temperature influences the performance and effectiveness of field and laboratory strains of the ichneumonid parasitoid, *Campoletis chlorideae*

Mukesh K. Dhillon · Hari C. Sharma

Received: 10 October 2008 / Accepted: 25 May 2009 / Published online: 11 June 2009

Abstract To understand the influence of temperature on host–parasitoid interactions as a consequence of climatic change, we studied development, survival, and fecundity of field and laboratory strains of the *Helicoverpa armigera* larval endoparasitoid, *Campoletis chlorideae* at five different temperatures under laboratory conditions. Post-embryonic development period and degree-days required for completing the life cycle by both the strains decreased by 2.5 and 1.5 folds at 27°C compared to 18°C. Post embryonic development period showed a negative ($r = -0.99$, $P < 0.001$) and the development rate a positive ($r = 0.99$, $P < 0.001$) association with an increase in temperature. However, no parasitoid larvae survived in *H. armigera* larvae reared at 12 and 35°C after parasitization, suggesting that temperatures ≥35°C as a result of global warming will be lethal for development and survival of immature stages of *C. chlorideae*. Adult longevity was negatively associated ($r = -0.91$ to -0.96, $P < 0.001$) with temperatures between 12 and 35°C. The parasitoid adults stored at 12°C survived for longer period and exhibited higher fecundity than those kept at 27°C, but the efficiency of parasitism and adult emergence were quite low. Sex ratio of the progeny at 12°C was highly male-biased than the insects kept at 27°C. Laboratory strain of the parasitoid exhibited better survival, and the adults lived longer than the field strain at 18°C than at 27°C. Therefore, *C. chlorideae* adults stored at 18°C could be used for parasitism, while the immature stages should be reared at 27°C for mass production of the parasitoid for biological control of *H. armigera*.

Keywords *Campoletis chlorideae* · *Helicoverpa armigera* · Temperature · Climatic change · Biological control

Handling Editor: Torsten Meiners.

M. K. Dhillon · H. C. Sharma (✉)
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh 502324, India
e-mail: h.sharma@cgiar.org

M. K. Dhillon
e-mail: m.dhillon@cgiar.org

Introduction

The ichneumonid parasitoid, *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae) is an important biocontrol agent of the noctuid pest, *Helicoverpa armigera* (Hubner) and other lepidopteran insects in pigeonpea [*Cajanus cajan* (L.) Millsp.], chickpea (*Cicer arietinum* L.), and cotton (*Gossypium* spp.) (Bhatnagar et al. 1982; Romeis and Shanower 1996; Dhillon and Sharma 2007a). It preferentially attacks second- and third-instar larvae of *H. armigera*, and the parasitoid larvae emerge from the fourth-instars for pupation. After oviposition, the parasitoid eggs hatch in 1.0–1.5 days inside the insect larvae and

complete development in 6–8 days at 27 ± 1°C and 65–85% R.H. (Sharma et al. 2008). On completion of development, the parasitoid larva emerges from the insect host, killing the latter in the process. It then weaves a cocoon around itself, and the pupal period lasts for 5–7 days. The life cycle is completed in 12–16 days (Sharma et al. 2008).

Parasitism of *H. armigera* larvae by *C. chlorideae* varies between 4% and 44% across regions, crops, and cropping systems (Pawar et al. 1989; Tikar et al. 2001), which might be because of variation in environmental conditions such as temperature, relative humidity, insect and crop hosts, and heterogeneity in insect populations. Thermal requirements and survival threshold also influence the activity and abundance of natural enemies, which in return influence the success of biological control programs (Butler and Lopez 1980; Chihrane et al. 1993; Bernal 1995). The likely increase in temperature as a result of climate change will have a great bearing on the effectiveness of natural enemies for pest management, which in turn will affect insect host–natural enemy associations, crop production, and food security. Therefore, the present studies were aimed at understanding the influence of different temperature regimes on post embryonic development, survival, and fecundity of the laboratory and field strains of the parasitoid, *C. chlorideae*. Such an information will also be useful to assess the effectiveness of the laboratory strain of the parasitoid, *C. chlorideae* in pest management under field conditions.

Materials and methods

Insect culture

The *H. armigera* larvae were reared on chickpea-based semi-synthetic artificial diet in the insectary at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India. The laboratory strain of the ichneumonid parasitoid, *C. chlorideae* was maintained on *H. armigera* larvae at 27 ± 1°C and 65–85% R.H. for over 50 generations (Dhillon and Sharma 2007a). Field culture (field strain) of the parasitoid was initiated from the cocoons collected from chickpea fields at the ICRISAT farm during the 2007 post-rainy season (October–March).

Influence of temperature on survival and development of *Campoletis chlorideae*

The influence of temperature on the parasitoid, *C. chlorideae* (laboratory and field strains) was studied under laboratory conditions. Five pre-mated *C. chlorideae* females from the laboratory and field strains were used for parasitizing *H. armigera* larvae reared on artificial diet as described previously. After parasitization, the *H. armigera* larvae were kept at 12 ± 1°C, 18 ± 1°C, 27 ± 1°C, 35 ± 1°C, and ambient conditions (where temperature varied between 12 and 25°C, averaging 23°C; hereafter mentioned as ambient conditions or 23°C), till emergence of parasitoid adults. Fifteen *H. armigera* larvae were parasitized in each replication, and there were six replications for each treatment in a completely randomized design ($N = 6$). Observations were recorded on larval and pupal periods, cocoon weight, percentage parasitism, adult emergence, and male and female weights to understand the influence of temperature on survival and development of the two strains of the parasitoid, *C. chlorideae*.

Effect of temperature on longevity and fecundity of *Campoletis chlorideae*

Freshly emerged adults (males and females) from the laboratory and field strains of *C. chlorideae* were kept at 12 ± 1°C, 18 ± 1°C, 27 ± 1°C, and 35 ± 1°C. One set of adults was kept under ambient conditions, where the temperature varied between 12 and 25°C (averaging 23°C). A total of 10 males and 10 females ($N = 10$) were placed in 2 l plastic jar cages (fitted with a wire-mesh screen on the top) under each temperature regime. The adults were provided with 10% honey solution as food in a cotton swab, and the food was changed on alternate days. Observations were recorded on longevity of *C. chlorideae* males and females under each temperature treatment.

The *C. chlorideae* adults kept at temperatures between 12 and 35°C revealed that the parasitoid adults can survive for 2–3 months at 12°C, and therefore, we planned an experiment to explore the possibility of maintenance of the parasitoid adults at low temperatures (12°C) over a longer period of time at low cost and labor in comparison to the normal rearing temperature (27°C). Six pairs of freshly

emerged males and females of *C. chlorideae* from the laboratory strain were kept in 2 l plastic jar cages at 12 ± 1°C and at 27 ± 1°C in the insect rearing laboratory ($N = 6$). The adults were provided with 10% honey solution as a food in a cotton swab. The adults were allowed to mate for three days prior to parasitization of *H. armigera* larvae. The *H. armigera* larvae reared on artificial diet in the laboratory were used for parasitization on alternate days, till all the females died. The parasitized *H. armigera* larvae were reared at 27 ± 1°C for recovery of the cocoons. Observations were recorded on fecundity (stabbings female^{-1}; number of stabbing = number of eggs laid), percentage parasitization (cocoon formation), adult emergence, longevity of males and females, and sex ratio.

Statistical analysis

The data were subjected to normality test and testing the homogeneity of variances, and the analysis of variance (ANOVA) was carried out using GenStat® 10th version statistical analysis program (Genstat 2008). The significance of differences between the treatments was judged by *F*-test, while the treatment means were compared using least significant differences (LSD) at $P \leq 0.05$. There was no survival of *C. chlorideae* in the *H. armigera* larvae kept at 12 and 35°C after parasitization, and these treatments were not included in the analysis of variance. The differences in survival and development parameters between laboratory and field strains of the parasitoid at a particular temperature were compared using paired *t*-tests. The association between temperature and developmental period and the longevity of parasitoid adults were computed using Spearman's correlation analysis. The relationship between temperature and developmental period, and developmental rate were computed using simple linear regression analysis. The degree-days were calculated using a modified formula given by Dhillon and Sharma (2007b).

Total degree-days for treatments under constant temperatures = Total development period (days) × storage temperature. Total degree-days for treatments under ambient conditions = Total development period (days) × average of minimum and maximum temperatures across the developmental period.

Results

Influence of temperature on survival and development of *Campoletis chlorideae*

Temperature showed a significant effect on larval ($F_{2,\ 10} = 1{,}352.05$, $P < 0.001$) and pupal ($F_{2,\ 10} = 1{,}297.44$, $P < 0.001$) periods of the parasitoid, *C. chlorideae*, and there was a significant and negative association between temperature and *C. chlorideae* larval ($r = -0.99$, $P < 0.001$) and pupal ($r = -0.98$, $P < 0.001$) periods. However, no parasitoid larvae survived in the *H. armigera* larvae kept at 12 and 35°C after parasitization. The parasitoid larvae took significantly more time to complete development at 18°C than at 23 and 27°C, which was significantly longer in laboratory strain than in the field strain across temperature regimes. The pupal period was also longer at 18°C when compared to the insects reared at 23 and 27°C. However, there were no significant differences between laboratory and field strains of the parasitoid for larval and pupal periods at a given temperature (Table 1). The linear regression analysis revealed a significant inverse relationship between temperature (T) and developmental period (DP) [laboratory strain (DP = 75.41–2.29T, $r = -0.99$, $P < 0.001$); field strain (DP = 73.71–2.25T, r = −0.99, $P < 0.001$)], while a significant and positive relationship was observed between temperature and developmental rate (DR) [laboratory strain (DR = −0.05 + 0.004T, $r = 0.99$, $P < 0.001$); field strain (DR = −0.05 + 0.004T, $r = 0.99$, $P < 0.001$)]. The temperature × strains interaction ($F_{2,\ 10} = 4.15$, $P = 0.028$) showed a significant influence on number of degree-days required by *C. chlorideae* to complete development, which was greater for the laboratory strain than for the field strain. Both field and laboratory strains of the parasitoid took significantly more numbers of degree-days at 18°C than at 23 and 27°C for completing development (Fig. 1). However, the differences between laboratory and field strains for the number of degree-days at a particular temperature were statistically non-significant at $P = 0.05$ (Fig. 1). Temperature showed significant effect ($F_{2,\ 10} = 8.54$, $P = 0.001$) on the cocoon weight, which was significantly greater in the laboratory strain, than that in the field strain under ambient conditions (Table 1).

The cocoon formation was significantly influenced by temperature ($F_{2,\ 10} = 8.21$, $P = 0.002$). Interaction

Table 1 Survival and development of laboratory and field strains of *Campoletis chlorideae* at different temperatures

Life table parameters/ temperature (°C)	Laboratory strain (Mean ± SE)	Field strain (Mean ± SE)	*t*-Value (*df* = 5)
Larval period (days)			
18	19.9 ± 0.19	18.8 ± 0.39	−2.40
23	11.5 ± 0.31	10.5 ± 0.21	−2.25
27	8.5 ± 0.06	8.5 ± 0.10	−0.48
Pupal period (days)			
18	15.4 ± 0.13	15.8 ± 0.45	1.55
23	9.1 ± 0.18	8.6 ± 0.24	−1.73
27	6.4 ± 0.10	6.3 ± 0.11	−1.05
Unit cocoon weight			
18	14.2 ± 0.42	13.9 ± 0.69	−0.46
23	13.7 ± 0.79	11.8 ± 0.53	−3.48*
27	12.4 ± 0.13	12.1 ± 0.70	−0.70
Cocoon formation (%)			
18	86.7 ± 2.11	82.7 ± 4.52	−0.84
23	74.7 ± 1.33	72.0 ± 5.74	−0.53
27	92.0 ± 4.90	78.7 ± 3.27	−5.47**
Adult emergence (%)			
18	74.7 ± 4.42	70.7 ± 4.99	−0.84
23	69.3 ± 3.40	53.3 ± 6.99	−3.37*
27	81.3 ± 3.89	54.7 ± 3.89	−4.67**
Adult male weight (mg)			
18	3.1 ± 0.08	2.6 ± 0.05	−5.56**
23	3.0 ± 0.08	3.1 ± 0.12	1.38
27	3.5 ± 0.06	3.2 ± 0.06	−4.02**
Adult female weight (mg)			
18	3.6 ± 0.18	3.0 ± 0.17	−1.63
23	3.1 ± 0.23	3.0 ± 0.10	0.04
27	4.4 ± 0.58	3.5 ± 0.23	−2.46

*, ** Values significant at $P \leq 0.05$ and 0.01, respectively. Figures presented in the table are mean values based on progenies of six adult parasitoids ($N = 6$)

effects of temperature × strains for adult emergence were significant ($F_{2,\ 10} = 5.26$, $P = 0.012$). The cocoon formation and adult emergence were significantly lower under ambient conditions (23°C) than at 18 and 27°C, suggesting a negative influence of fluctuating temperatures on survival of the parasitoid. There were no significant differences in cocoon formation between laboratory and field strains at 18 and 23°C, but it was significantly lower in the field strain than in the laboratory strain at 27°C (Table 1). Adult emergence was significantly greater in the

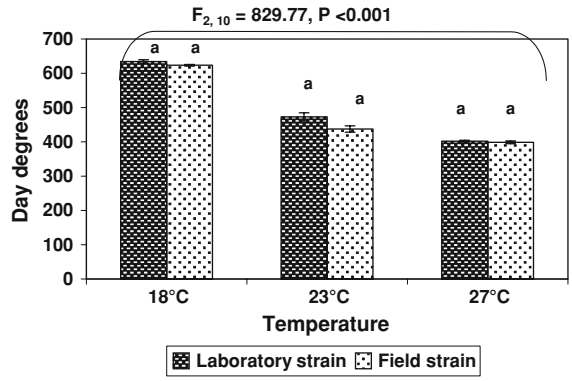

Fig. 1 Day degrees (mean ± SE) required for completing development of the laboratory and field strains of the parasitoid, *Campoletis chlorideae*. The paired bars following the same letter are non-significant at $P \leq 0.05$

laboratory strain than in the field strain of the parasitoid at 23 and 27°C, thereby suggesting greater resilience of the laboratory strain at temperatures between 18 and 27°C (Table 1). Temperature showed a significant effect on the weight of the parasitoid females ($F_{2,\ 10} = 8.19$, $P = 0.002$), which was significantly greater at 27°C (3.98 ± 0.21 mg female^{-1}) than at 23 and 18°C. Temperature × strain indicated significant interaction effects ($F_{2,\ 10} = 15.63$, $P < 0.001$) for weight of adult males. The weights of the laboratory strain males were significantly greater than those of the field strain at 18 and 27°C. However, there were no significant differences in the female weights of the parasitoid (Table 1).

Effect of temperature on longevity and fecundity of *Campoletis chlorideae*

Longevity of *C. chlorideae* males was significantly influenced by temperature ($F_{4,\ 36} = 150.91$, $P < 0.001$). Temperature × strain interaction was significant for longevity of the parasitoid females ($F_{4,\ 36} = 25.97$, $P < 0.001$). The longevity of males and females of both the strains decreased with an increase in temperature from 12 to 35°C. Maximum longevity of both males and females was recorded at 12°C (Table 2). There was a significant and negative association between temperature and longevity of *C. chlorideae* males ($r = -0.94$ to -0.95, $P < 0.001$) and females ($r = -0.91$ to -0.96, $P < 0.001$) at 12 to 35°C. There were no significant differences in

Table 2 Effects of temperature on longevity (days) of laboratory and field strains of *Campoletis chlorideae* adults

Temperature (°C)	Male			Female		
	Laboratory strain (mean ± SE)	Field strain (mean ± SE)	Mean (mean ± SE)	Laboratory strain (mean ± SE)	Field strain (mean ± SE)	Mean (mean ± SE)
12	63.7 ± 5.2	55.2 ± 3.8	59.5 ± 4.5	90.9 ± 5.7	70.7 ± 6.8	80.8 ± 6.3
18	41.2 ± 3.1	48.1 ± 3.6	44.7 ± 3.4	39.8 ± 7.0	60.3 ± 3.6	50.1 ± 5.3
23	18.2 ± 4.4	20.2 ± 2.8	19.2 ± 3.6	11.8 ± 4.9	29.3 ± 2.9	20.6 ± 3.9
27	14.9 ± 1.4	14.2 ± 2.9	14.6 ± 2.2	18.0 ± 0.6	19.8 ± 0.7	18.9 ± 0.7
35	5.7 ± 0.8	4.4 ± 0.2	5.1 ± 0.5	3.5 ± 0.8	3.8 ± 0.8	3.7 ± 0.8
Mean	28.7 ± 7.5	28.4 ± 6.7	–	32.8 ± 9.5	36.8 ± 7.4	–

LSD ($P = 0.05$) for comparing	Temperature	Strain	Strain × temperature	Temperature	Strain	Strain × temperature
	5.19	NS	NS	4.49	2.84	6.35

NS Nonsignificant at $P \leq 0.05$. Figures presented in the table are mean values based on ten adult parasitoids ($N = 10$)

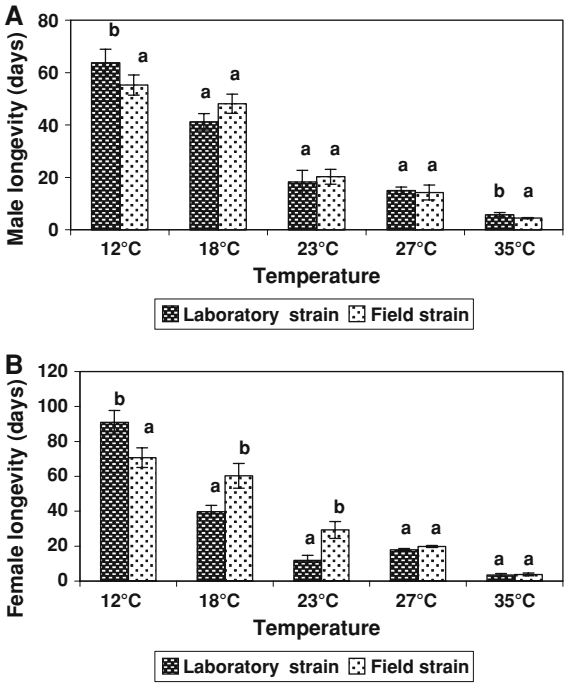

Fig. 2 Effects of temperature on longevity (mean ± SE) of laboratory and field strains of *Campoletis chlorideae* adults (**A**: males; **B**: females). The temperatures under ambient conditions ranged between 12 to 25°C (average 23°C) during the experimental period. The paired bars following the same letter are non-significant at $P \leq 0.05$

longevity of parasitoid males between laboratory and field strains. The males of the laboratory strain lived significantly longer than that of the field strain at 12 and 35°C (Fig. 2A). The females of the laboratory strain lived longer than the field strain at 12°C, while the longevity of field strain females was longer than the laboratory strain females at 18 and 23°C (Fig. 2B). However, the differences in longevity of parasitoid females between laboratory and field strain at 27 and 35°C were non-significant at $P = 0.05$.

There was a significant influence of temperature on fecundity ($F_{1,\ 5} = 29.06$, $P = 0.003$), parasitism potential ($F_{1,\ 5} = 57.16$, $P < 0.001$), adult emergence ($F_{1,\ 5} = 127.71$, $P < 0.001$), longevity of males ($F_{1,\ 5} = 108.01$, $P < 0.001$) and females ($F_{1,\ 5} = 63.99$, $P < 0.001$), and sex ratio ($F_{1,\ 5} = 353.82$, $P < 0.001$) in the progenies of laboratory strain of *C. chlorideae*. Fecundity of the *C. chlorideae* females kept at 12°C was greater than those kept at 27°C (Table 3). However, percent parasitism and adult emergence in the progenies of insects kept at 12°C were lower than those kept at 27°C. The progeny sex ratio was female-biased at 27°C and male-biased at 12°C (Table 3). Longevity of males was greater than that of the females at 12°C, while the reverse was true at 27°C. However, both males and females lived longer at 12°C than at 27°C.

Discussion

Deviation in temperature above and below the insect's survival threshold results in adverse effects on their metabolic rate, physiological responses, and survival and development (Wilson and Barnett 1983;

Table 3 Effect of temperature on adult longevity, progeny production, survival, and sex ratio of *Campoletis chlorideae*

Biological parameters	Temperature (°C)		*t*-Value ($df = 5$)
	12 (Mean ± SE)	27 (Mean ± SE)	
Fecundity (stabbing female^{-1})	262.8 ± 12.94	217.6 ± 10.64	5.39**
Parasitization (%)	56.0 ± 2.79	92.0 ± 4.90	−7.54**
Adult emergence (%)	39.2 ± 2.25	81.3 ± 3.89	−11.30**
Male longevity (days)	68.8 ± 6.58	18.0 ± 1.14	10.39**
Female longevity (days)	58.4 ± 5.55	24.4 ± 0.60	8.00**
Sex ratio (M:F)	0.34 ± 0.06	1.38 ± 0.03	−18.81**

** Values significant at $P \leq 0.01$. Figures presented in the table are mean values based on progenies of six adult parasitoids ($N = 6$).
SE Standard error of mean

Sinclair et al. 2003). As the temperature reaches upper or lower lethal limit, the rate of metabolism and development decreases. However, metabolism and development rates increase normally with an increase in temperature within the optimal survival range. Changes in temperature above or below the threshold levels influence both growth and development of the insect host, which in turn results in asynchrony in growth and development, leading to reduced survival of the endoparasitoid. Temperature requirements for growth and development of the parasitoid in relation to the host have been reported earlier by Miller and Gerth (1994). The parasitoid–host relationship is highly influenced by temperature (McClure 1978; Dowell 1979), and is considered as one of the critical factors for survival and development of the immature stages of the parasitoids. Development of parasitoids is prolonged and mortality increases at relatively cool and hot temperature extremes (Ables et al. 1976; Cave and Gaylor 1988; Miller 1996). In case of *C. chlorideae*, we observed an inverse relationship between temperature and developmental period and a positive relationship between temperature and developmental rate for both laboratory and field strains of the parasitoid within the survival range. No parasitoid larvae emerged from the *H. armigera* larvae reared at 12 or 35°C after parasitization, which may be due to asynchrony between the development of host and the parasitoid larvae, thereby suggesting that temperatures ≤12 or ≥35°C are lethal for the survival and development of the immature stages of the parasitoid, *C. chlorideae*. Similar temperature-thresholds for survival and development of *C. chlorideae* have also been observed by several workers (Nandihalli 1994; Raju et al. 2001; Teggelli et al. 2004). However, Pandey and Tripathi (2008) reported 24.6 and 9.4 days as the developmental periods of the parasitoid, *C. chlorideae* at 12 and 37°C, respectively, while *H. armigera* larval development takes 2 months at 13.3°C (4th instar at about 45–48 days) and 11 days at 32.5°C (4th instar at about 8–8.5 days) (Jallow and Matsumura 2001), and this will probably result in a mismatch between the host and parasitoid development. Another possible reason for such differences could be the differences in strains of *C. chlorideae* and humidity regimes.

A decrease in developmental period with an increase in temperature between 20 and 32°C has earlier been reported for *C. chlorideae* (Teggelli et al. 2004); citrus leaf miner, *Phyllocnistis citrella* Stainton larval parasitoid, *Pnigalio pectinicornis* L. (Kalaitzaki et al. 2007); and *Bemisia tabaci* (Gennadius) endoparasitoid, *Eretmocerus* sp. nr. *furuhashii* Rose & Zolnerowich (Qiu et al. 2007). *Campoletis chlorideae* required 2.5-fold less time to complete development at 27°C than at 18°C. The parasitoid adults are also exposed to the external environment, which may have direct effect on the adult parasitoids and indirect effects on their progeny. Longevity of both field and laboratory strains of the parasitoid decreased with an increase in temperature from 12°C to 35°C. Shorter life span of *Campoletis predistinctus* (Ashmead) adults has earlier been observed at high temperatures (Hoelscher and Vinson 1971). Cocoon formation and adult emergence were lower under ambient conditions (23°C) than at 18 and 27°C, indicating that fluctuating temperatures have an adverse effect on survival of the parasitoid. Therefore, biological control agents need to be selected to

tolerate extreme temperatures under natural conditions to avoid incompatibility with harsh climates under field conditions.

At very high temperatures, mating frequency is reduced, while at lower temperatures, the adults may fail to mate (Cook 2007). There is low or no oviposition by tobacco budworm, *Heliothis virescens* (F.) at low temperatures (Henneberry and Clayton 1991). Egg hatch in *H. armigera* is also influenced by temperatures below the lower and upper thresholds (Dhillon and Sharma 2007b). Longevity of tobacco budworm, *H. virescens* and the egg parasitoid, *Trichogramma* spp. adults decreases with an increase in temperature (Henneberry and Clayton 1991; Maceda et al. 2003). Temperature had a significant influence on fecundity, parasitism potential, adult emergence, and sex ratio of *C. chlorideae*. The parasitoid adults kept at 12°C survived >30 days longer, had greater fecundity, but poor parasitism potential, and the sex ratio was male-biased in the progenies. This might be because of mating disruption, false stabbings (stabbing without egg laying), or impact of low temperatures on development of the parasitoid eggs (Hoelscher and Vinson 1971; King 1987, 1996).

Temperature exercises a significant influence on host–parasitoid interaction, and such an information will be useful to assess the effects of climatic change on the effectiveness of biological control agents. Laboratory strain of *C. chlorideae* showed better survival and lived longer at 18°C than at 27°C. Therefore, parasitoid adults stored at 18°C could be used for parasitism, while the immature stages should be reared at 27°C for mass production of the parasitoid for biological control of *H. armigera*.

Acknowledgments The technical support of Messrs V. Venkateshwara Rao and S. V. N. Chandra and funding by the Indo-Swiss Collaboration on Biotechnology (ISCB), Swiss Agency for Development and Cooperation (SDC), Berne, Switzerland, and the Department of Biotechnology (DBT), New Delhi, India, are gratefully acknowledged.

References

Ables JR, Shepard M, Holman JR (1976) Development of the parasitoids *Spalangia endius* and *Muscidifurax raptor* in relation to constant and variable temperature: simulation and validation. Environ Entomol 5:329–332

Bernal JS (1995) An ecological basis for the field performances of two exotic parasites (Hymenoptera: Aphidiidae et Aphelinidae) of the Russian wheat aphid (*Diuraphis noxia* Mordwilko, Homoptera: Aphididae). PhD thesis, University of California, Riverside, USA

Bhatnagar VS, Lateef SS, Sithanantham S, Pawar CS, Reed W, (1982) Research on *Heliothis* at ICRISAT. In: Reed W and Kumble V (eds) Proceedings of the International Workshop on *Heliothis* Management, 15–20 November 1981. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India. pp 385–395

Butler GD Jr, Lopez JD (1980) *Trichogramma pretiosum*: development in two hosts in relation to constant and fluctuating temperatures. Ann Entomol Soc America 73:671–673

Cave RD, Gaylor MJ (1988) Influence of temperature and humidity on development and survival of *Telenomus reynoldsi* parasitizing *Geocoris punctipes* eggs. Ann Entomol Soc America 81:278–285

Chihrane J, Laugé G, Hawlitzky N (1993) Effects of high temperature shocks on the development and biology of *Trichogramma brassicae* (Hym.: Trichogrammatidae). Entomophaga 38:185–192

Cook DF (2007) Influence of temperature on copula duration and mating propensity in *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae). Australian J Entomol 33:5–8

Dhillon MK, Sharma HC (2007a) Survival and development of *Campoletis chlorideae* on various insect and crop hosts: Implications for *Bt*-transgenic crops. J Appl Entomol 131: 179–185

Dhillon MK, Sharma HC (2007b) Effect of storage duration and temperature on viability of eggs of *Helicoverpa armigera* (Lepidoptera: Noctuidae). Bull Entomol Res 97:55–59

Dowell RV (1979) Synchrony and impact of *Amitus hesperidum* on its host, *Aleurocanthus woglumi* in southern Florida. Entomophaga 24:221–227

GenStat (2008) Introduction to GenStat for Windows®. Genstat, 10th edn. Lawes Agricultural Trust, Rothamsted Experimental Station

Henneberry TJ, Clayton TE (1991) Tobacco budworm (Lepidoptera: Noctuidae): temperature effects on mating, ovipositon, egg viability, and moth longevity. J Econ Entomol 84:1242–1246

Hoelscher CE, Vinson SB (1971) The sex ratio of hymenopteran parasitoid, *Campoletis predistinctus*, is affected by photoperiod, mating and temperature. Ann Entomol Soc America 64:1373–1376

Jallow MFA, Matsumura M (2001) Influence of temperature on the rate of development of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). Appl Entomol Zool 36:427–430

Kalaitzaki AP, Lykouressis DP, Perdikis ChD, Alexandrakis VZ (2007) Effect of temperature on development and survival of the parasitoid *Pnigalio pectinicornis* (Hymenoptera: Eulophidae) reared on *Phyllocnistis citrella* (Lepidoptera: Gracillariidae). Environ Entomol 36: 497–505

King BH (1987) Offspring sex ratios in parasitoid wasps. Q Rev Biol 62:367–395

King BH (1996) Sex ratio responses to other parasitoid wasps: multiple adaptive explanations. Behav Ecol Sociobiol 39:367–374

Maceda A, Hohmann CL, dos Santos HR (2003) Temperature effects on *Trichogramma pretiosum* Riley and *Trichogrammatoidea annulata* De Santis. Brazilian Arch Biol Tech 46:1–11

McClure MS (1978) Seasonal development of *Fiorinia externa*, *Tsugaspidiotus tsugae* (Homoptera: Diaspididae), and their parasite, *Aspidiotiphagus citrinus* (Hymenoptera: Aphelinidae): importance of parasite-host synchronism to the population dynamics of two scale pests of hemlock. Environ Entomol 7:863–870

Miller JC (1996) Temperature-dependent development of *Meteorus communis* (Hymenoptera: Braconidae), a parasitoid of the variegated cutworm (Lepidoptera: Noctuidae). J Econ Entomol 89:877–880

Miller JC, Gerth W (1994) Temperature-dependent development of *Aphidius matricariae* as a parasitoid of the Russian wheat aphid. Environ Entomol 23:1304–1307

Nandihalli BS (1994) Ecology of an egg parasitoid *Trichogramma chilonis* Ishii and a larval parasitoid *Campoletis chlorideae* Uchida, of the oriental bud worm, *Helicoverpa assulta* (Guenee). PhD thesis, Seoul National University, Seoul, Korea

Pandey AK, Tripathi CPM (2008) Effect of temperature on the development, fecundity, progeny sex ratio and life-table of *Campoletis chlorideae*, an endolarval parasitoid of the pod borer, *Helicoverpa armigera*. BioControl 53:461–471

Pawar CS, Bhatnagar S, Jadhav DR (1989) *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae) as a parasite of *Helicoverpa armigera* (Hub.) (Lepidoptera: Noctuidae) in southwest India. Proc Indian Acad Sci (Animal Sci) 95:695–703

Qiu BL, De Barro PJ, Ren SX, Xu CX (2007) Effect of temperature on the life history of *Eretmocerus* sp nr. *furuhashii*, a parasitoid of *Bemisia tabaci*. BioControl 52:733–746

Raju GT, Biradar AP, Balikai RA, Rao KJ (2001) Effect of temperature, relative humidity and their interactions on the development of *Campoletis chlorideae* Uchida. Adv Agril Res, India 16:49–53

Romeis J, Shanower TG (1996) Arthropod natural enemies of *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) in India. Biocontr Sci Tech 6:481–508

Sharma HC, Dhillon MK, Arora R (2008) Effects of *Bacillus thuringiensis* δ-endotoxin-fed *Helicoverpa armigera* on the survival and development of the parasitoid *Campoletis chlorideae*. Entomol Exp Appl 126:1–8

Sinclair BJ, Vernon P, Klok CJ, Chown SL (2003) Insects at low temperatures: an ecological perspective. Trends Ecol Evol 18:257–262

Teggelli RG, Rao KJ, Kulkarni KA (2004) Effect of temperature and relative humidity and their interactions on the development of *Campoletis chlorideae* Uchida. Karnataka J Agril Sci 17:476–478

Tikar SN, Rao NGV, Satpute NS, Dandale HG (2001) Egg laying preference and larval parasitization of *Helicoverpa armigera* (Hubner) on weed host *Lagascea mollis* (Cav) in comparison with cotton at Akola. Insect Environ 6:180–181

Wilson LT, Barnett WW (1983) Degree-days: an aid in crop and pest management. California Agric (USA) 37:4–7