

Thermal Requirements and Parasitism Capacity of *Trissolcus brochymenae* (Ashmead) (Hymenoptera: Scelionidae) Under Constant and Fluctuating Temperatures, and Assessment of Development in Field Conditions

J. B. TORRES,¹ D. L. MUSOLIN² AND J. C. ZANUNCIO³

¹DEPA-Fitossanidade, Universidade Federal Rural de Pernambuco. Av. Dom Manoel de Medeiros S/N—Dois Irmãos, 52171-900 Recife, PE, Brasil;

²Biological Research Institute of St. Petersburg State University, Oranienbaumskoye sh., 2, Stary Peterhof, St. Petersburg, 198904, Russia;

³DBA-Universidade Federal de Viçosa, 36571-000 Viçosa, MG, Brasil

(Received 22 June 2001; accepted 26 April 2002)

In order to understand the relative importance of Trissolcus brochymenae, a common egg parasitoid of the predatory stinkbug Podisus nigrispinus in areas where this predator is released, the thermal requirements and developmental periods (egg to adult) at constant (17, 20, 25, 28 and 32°C) and fluctuating (10–20, 13–23, 15–25, 17–27, 20–30 and 25–35°C) temperatures, and the effect of constant and fluctuating temperatures systems on the longevity and parasitism capacity of T. brochymenae were investigated. Based on thermal requirements of the parasitoid and field day/night temperature variation in the regions where P. nigrispinus was released, we calculated monthly and yearly number of generations of the parasitoid. Parameters of biological and thermal requirements of T. brochymenae were not affected when the insects were reared under constant or fluctuating temperatures. It was shown that males have a shorter developmental period and lower thermal requirements than females. The lowest parasitism capacity and shortest longevity of T. brochymenae were observed under fluctuating temperature regimes of 10–20°C and 25–35°C. A higher parasitism capacity was obtained under a 20–30°C regime (96.0 ± 33.6 offspring per female), while longevity was longer at a constant temperature of 27°C (17.6 ± 0.6 days). T. brochymenae showed a continuous development during all seasons through the year under field conditions, accomplishing 2.7, 2.4, 2.9 generations per month in the CAF, Pains, and Refloralje areas. An average of 26.4 and 25.8, 25.8 and 25.3, and 24.7 and 23.6 generations per year under constant and fluctuating temperatures systems was estimated for the CAF, Pains, and Refloralje areas, respectively. No significant difference between thermal systems in each area was observed; however, a significantly smaller number of generations per year were estimated to occur in the Refloralje area. Implications of these results for the forecasting of parasitoid population development and its impact on the host stinkbug predator are discussed.

Correspondence to: J. B. Torres. Present address: Department of Entomology, University of Georgia, Athens, GA 30602–2603, USA. E-mail: jtorres@bugs.ent.uga.edu

Keywords: *Asopinae*, *biological control*, *egg parasitoid*, *Podisus nigrispinus*, *Trissolcus brochymenae*, *parasitism rate*, *forest entomology*

INTRODUCTION

At present, biocontrol programs in Brazil emphasize the use of natural enemies to reduce the frequency and attenuate the severity of outbreaks of insect pests in *Eucalyptus* forest ecosystems. In a multipest ecosystem such as *Eucalyptus*, with the simultaneous occurrence of many lepidopteran species, the application of biocontrol programs based on seasonal inoculative release of pest-specific natural enemies becomes very expensive and complex. Therefore, mass rearing and release programs applying the generalist stinkbug predator *Podisus nigrispinus* (Dallas) have been performed by forest companies to control defoliator caterpillars in Brazil (Zanuncio *et al.*, 1994a,b; Torres *et al.*, 1996a). However, this program has shown the need for additional research to investigate ecological factors affecting field maintenance of this predator. The development of a biological control program with *P. nigrispinus* needs to take a number of factors into account in order to be successful in use. Parasitoids of *P. nigrispinus* were reported to be an important biotic factor reducing natural populations of the predator in eucalyptus plantations (Torres *et al.*, 1996a, 2001). The indigenous scelionid *Trissolcus brochymenae* (Ashmead) is one the most common egg parasitoids of stinkbug predators in soybeans (Corrêa-Ferreira & Moscardi, 1995) and in eucalyptus plantations (Barcelos *et al.*, 1994; Torres *et al.*, 1996a) in Brazil. It has been reported as the major mortality factor of *P. nigrispinus* eggs, especially in areas where the stinkbug predator has been repeatedly released for biocontrol of eucalyptus caterpillar populations for a long time (Torres *et al.*, 2001). This parasitoid has been recorded from *Brontocoris tabidus* (Signoret), *Podisus sculptus* (Distant), *P. nigrispinus*, *Nezara viridula* L., *Euchistus heros* (Fab.), *Piezodorus guildinii* (Westwood), *Thyanta perditor* (Fab.), *Acrosternum* spp., *Dichelops furcatus* (Fab.), and *Dichelops melacanthus* (Fab.) (Yeagan, 1979; Orr *et al.*, 1985; Barcelos *et al.*, 1994; Corrêa-Ferreira & Moscardi, 1995; Torres *et al.*, 1996a,b; Zanuncio *et al.*, 2000).

Mathematical models based on thermal requirements, degree-days, and threshold temperature have been used to predict the occurrence of insect pests and natural enemies, migration and colonization of new areas, and as support for rearing facilities (Wagner *et al.*, 1984; Higley *et al.*, 1986; Miller, 1992; Peterson & Meyer, 1994; Torres *et al.*, 1998). Based on average temperatures from the north of Minas Gerais State, Brazil, where *P. nigrispinus* has been released by forest companies, Torres *et al.* (1997) estimated that *T. brochymenae* can develop during all seasons in the field, with twice as many generations as its host, *P. nigrispinus*. Nevertheless, an adequate frequency of releases can reduce the heavy parasitism of *P. nigrispinus* that is often recorded at the end of caterpillar outbreaks (Torres *et al.*, 1996a). Due to the importance of *Podisus* spp. as biological control agents, there is interest in understanding the impact of *T. brochymenae* on their populations. One way to evaluate the potential of *T. brochymenae* to reduce *Podisus* spp. population growth is to develop a population model of the parasitoid-host interaction. However, the thermal requirements and reproductive success of the parasitoids must be determined before realistic estimates of host and parasitoid population growth can be made.

Several biological characteristics contribute to the efficacy of an insect parasitoid. Thus, searching ability, fecundity, longevity and sex ratio are important factors that are directly affected by local temperature. In addition, the availability of alternative hosts for *T. brochymenae* has been claimed to increase its prevalence (Barcelos *et al.*, 1994; Corrêa-Ferreira & Moscardi, 1995; Torres *et al.*, 1996a, Zanuncio *et al.*, 2000).

Therefore, to improve the current knowledge of the effects of *T. brochymenae* on the stinkbug predator, experiments were undertaken to evaluate developmental rates, thermal requirements, parasitism capacity, and longevity at given constant and fluctuating temper-

atures (simulating maximum and minimum of the day and night temperature variation in three reforested areas in the north of Minas Gerais State, Brazil). The results were used to estimate the number of generations of this parasitoid per month and year.

MATERIALS AND METHODS

Insect

The stinkbug predator *P. nigrispinus* was cultured in the laboratory on *Musca domestica* L., according to the method of Zanuncio *et al.* (1994a). The parasitoid *T. brochymenae* was obtained from field collections, using stinkbug predator egg masses left for parasitizing during three days in a eucalyptus plantation in the north of Minas Gerais State, Brazil. The culture was maintained on eggs of *P. nigrispinus* in small vials with a drop of honey at $27 \pm 1^\circ\text{C}$, 60–70% relative humidity (RH), and a photophase of 14:10 (L:D) h. Voucher specimens of both species are deposited at the Biological Control Laboratory of the Federal Rural University of Pernambuco, Pernambuco State, Brazil.

Developmental Period and Thermal Requirements of *T. brochymenae*

The effects of temperature on the developmental period and the thermal requirements of *T. brochymenae* were studied under five constant temperatures of 17, 20, 25, 28 and 32°C , and under six fluctuating temperatures of 10–20, 13–23, 15–25, 17–27, 20–30 and $25\text{--}35^\circ\text{C}$. Fluctuating temperatures were chosen to cover the range of the temperatures in different seasons of the year: 10–20 and $13\text{--}23^\circ\text{C}$ (winter), $15\text{--}25^\circ\text{C}$ (winter–autumn), 17–27 and $20\text{--}30^\circ\text{C}$ (spring–summer) and $25\text{--}35^\circ\text{C}$ (summer). These temperatures were based on maximum and minimum average temperatures for each month over 10 years by three forest companies, i.e. CAF Florestal, Pains Florestal and Refloralje, in the North Region of Minas Gerais State, Brazil. All temperature treatments were conducted under photoperiods of 14:10 (L:D) h, and 60–70% RH. The higher fluctuating temperatures were associated with photophase and lower with scotophase, so providing shorter period at the low temperature, as would occur under field conditions. To determine the duration of development of *T. brochymenae*, 1-day-old *P. nigrispinus* egg masses (15–20 eggs per egg mass) were exposed to one 1-day-old mated *T. brochymenae* females for 6 h at 27°C . Egg masses were then placed in separate tubes and incubated in climatic chambers at each experimental temperature regime described above, and checked twice a day at fixed times until adult emergence. Each treatment was replicated 10 times (females). Egg to adult development, emergence rate (percentage of egg-adult survival), sex ratio (percentage of females in offspring) and thermal requirements of *T. brochymenae* were evaluated in both thermal systems studied (constant and fluctuating temperatures). All data were analyzed using one-way analysis of variance (ANOVA), and Tukey's test (at $P = 0.05$) was carried out for comparison of means using Statistica 5.0 (StatSoft, 1995). Degree-days (DD) and threshold temperature (t_i) were determined from a linear regression of development rate y (the reciprocal of time spent in days from oviposition to adult parasitoid emergence) on temperature ($^\circ\text{C}$), $t, y_i = b_i t + a_i$. Threshold temperatures (t_i) were estimated by extrapolating the regression line and recording where they cut the temperature axis (e.g. $t_i = -a_i/b_i$). The DD above the t_i required to complete development were estimated from the reciprocal of the slope of the fitted regression line.

Effect of Constant and Fluctuating Temperatures on Longevity and Fecundity of *T. brochymenae*

In each experimental temperature regime, parasitized egg masses of *P. nigrispinus* were separated and placed into small vials. After emergence, male-female pairs of *T. brochymenae* were isolated in separate glass tubes (25×90 mm), and provided with a drop of honey.

Parasitoids were also provided daily with 10–15 1-day-old *P. nigrispinus* eggs throughout the life of each female. This number of eggs per female per day has proved to be enough (Torres *et al.*, 1996b). Exposed egg masses were held under one constant temperature (27°C) and six fluctuating temperatures (10–20, 13–23, 15–25, 17–27, 20–30 and 25–35°C), at 60–70% RH and photoperiod of 14:10 (L:D) h. The lower temperature levels were set up during the dark period (10 h) and higher temperature levels as light time (14 h). Twenty pairs of 1-day-old *T. brochymenae* were used for each temperature treatment. Upon emergence, nymphs of *P. nigrispinus* were removed and the number of parasitized eggs was recorded in each egg mass. Parasitism (number of offspring), longevity, emergence rate and sex ratio were also calculated for *T. brochymenae*. Statistical analysis of the data sets was performed using the computer Statistica 3.0 program and differences among temperatures were tested with a Tukey test at $P = 0.05$ (StatSoft, 1995).

Number of Generations Under Field Temperature Conditions

Possible numbers of generations of *T. brochymenae* were estimated for the geographical areas where an association of the egg parasitoid and its host *P. nigrispinus* has been observed (Torres *et al.*, 1996a). Day and night temperatures were recorded from 1988 to 1993 in three areas of eucalyptus forest where *P. nigrispinus* had been released for eucalyptus defoliator control. The number of generations of *T. brochymenae* females per month and the total number of generations per year were assessed from a relationship between thermal requirements previously determined in the laboratory under constant and fluctuating temperatures by the formula: $GN = [T/(DD/(t_f - t_t))]$, where T is the time considered, i.e. month (30 days) or year (365 days), DD is degree-days, t_t is threshold temperature (parameters previously determined in the laboratory under temperature based on field estimated temperature variations), and t_f is average field temperature (the average of temperature variation considering maximum average daily temperature and minimum average nightly temperature associated with a photoperiod of 14:10 (L:D) h). Numbers of generations estimated per year under constant and fluctuating temperatures and in different areas were analyzed by one-way ANOVA and compared by Tukey's test at 0.05 level of significance (StatSoft, 1995).

RESULTS

Developmental Period and Thermal Requirements

Developmental period (egg exposure to parasitism to emergence of adult parasitoid) in *T. brochymenae* decreased when constant temperatures increased from 17 to 32°C for both males and females ($F = 33.12$; $df = 4, 45$; $P < 0.001$). A similar pattern was recorded when fluctuating temperatures increased from 10–20 to 25–35°C ($F = 22.04$; $df = 5, 54$; $P < 0.001$). However, the developmental period was similar at constant temperatures of 28 and 32°C, whereas a continuous decrease was registered at fluctuating temperatures for both males and females (Table 1). In addition, at fluctuating temperatures *T. brochymenae* showed a development slightly slower with high standard error than that at constant temperatures (Table 1). For both thermal systems, developmental periods of males were approximately one day shorter than those of females at higher temperatures and four days shorter at lower levels temperatures (Table 1).

There were no significant differences in emergence rate at different constant or fluctuating temperatures (Table 1). Likewise, the sex ratio of *T. brochymenae* was not affected by either constant ($F = 0.32$; $df = 4, 45$; $P > 0.05$) or fluctuating temperatures ($F = 1.12$; $df = 5, 54$; $P > 0.05$) (Table 1); it ranged from 88 to 91% females at constant and from 87 to 90% females at fluctuating temperatures (Table 1).

Degree-days and threshold temperatures for *T. brochymenae* were similar when they were estimated based on constant or fluctuating temperatures (Table 2). The degree-days estimated

TABLE 1. Developmental period (egg-adult), emergence rate, and sex ratio of *T. brochymenae* reared on *P. nigrispinus* eggs at five constant and six fluctuating temperatures

| Temperature (°C) | Developmental period (days) ^a | | Emergence rate (%) | Sex ratio |
|----------------------------|--|-------------|--------------------|-----------|
| | Female | Male | | |
| Constant | | | | |
| 17 | 35.4 ± 0.7a | 31.8 ± 1.8a | 92.7 ± 4.9a | 0.90a |
| 20 | 19.1 ± 0.1b | 17.3 ± 0.3b | 90.0 ± 9.4a | 0.88a |
| 25 | 13.0 ± 0.1c | 12.0 ± 0.0c | 89.0 ± 6.4a | 0.89a |
| 28 | 11.1 ± 0.1d | 10.0 ± 0.0d | 92.3 ± 7.2a | 0.89a |
| 32 | 10.2 ± 0.1d | 9.0 ± 0.4d | 89.3 ± 9.0a | 0.91a |
| Fluctuating | | | | |
| 10–20 (15.83) ^b | 48.4 ± 0.4a | 44.9 ± 0.5a | 91.2 ± 9.1a | 0.88a |
| 13–23 (18.83) | 25.6 ± 1.7b | 23.7 ± 1.1b | 85.5 ± 7.4a | 0.90a |
| 15–25 (20.83) | 23.1 ± 0.4b | 20.8 ± 0.7b | 80.3 ± 8.4a | 0.89a |
| 17–27 (22.83) | 16.6 ± 0.8c | 14.6 ± 0.6c | 86.2 ± 9.0a | 0.88a |
| 20–30 (25.83) | 13.3 ± 0.2d | 12.3 ± 0.2d | 91.6 ± 2.6a | 0.87a |
| 25–35 (30.83) | 11.2 ± 0.3e | 10.5 ± 0.5e | 88.7 ± 10.5a | 0.89a |

^aMean ± SE within a column having an identical letter for constant and fluctuating temperatures regimes are not significantly different at the 0.05 level by Tukey test.

^bMean temperature under the fluctuating regimes.

TABLE 2. Degree-days (DD), threshold temperatures (t_i) and respective coefficients of determination (r^2) for *T. brochymenae* reared on *P. nigrispinus* eggs at five constant and six fluctuating temperatures regimes

| Thermal system | Sex | K (DD) | t_i (°C) | r^2 (%) |
|-------------------------|--------|--------|------------|-----------|
| Constant temperature | Female | 214.7 | 9.5 | 95.75 |
| | Male | 189.2 | 9.8 | 97.12 |
| Fluctuating temperature | Female | 213.2 | 10.0 | 97.43 |
| | Male | 200.7 | 9.7 | 96.30 |

for males and females were 189.2 and 214.7 at constant and 200.7 and 213.2 at fluctuating temperatures, respectively (Table 2). Males achieved higher rates of development when reared at both constant and fluctuating temperatures as described by equations of regression: $y = -0.0522 + 0.00528x$, $r^2 = 0.97$, $P < 0.05$ and $y = -0.0483 + 0.00497x$, $r^2 = 0.96$, $P < 0.05$ (constant and fluctuating temperatures, respectively). Females required more degree-days to develop: $y = -0.0449 + 0.0047x$, $r^2 = 0.95$, $P < 0.05$, and $y = -0.0469 + 0.00468x$, $r^2 = 0.97$, $P < 0.05$ (at constant and fluctuating temperatures, respectively).

Fecundity and Longevity of Mated Females

Fecundity of *T. brochymenae* was affected by alternating temperatures ($F = 45.09$; $df = 6, 133$; $P < 0.0001$) (Figure 1). A similar fecundity was achieved at 20–30°C (mean ± SD, 96.0 ± 33.6 offspring) followed by 17–27°C (73.1 ± 15.3 offspring) and a constant temperature of 27°C (69.6 ± 9.2 offspring) and higher values than 10–20, 13–23, 15–25 and 25–35°C temperature regimes. A fecundity of 24.1 ± 6.5 offspring at the lowest winter temperature (10–20°C) was recorded (Figure 1). These results show that parasitism can occur during all four seasons of the year.

The longevity of mated females reared on *P. nigrispinus* eggs did not show a pattern related to temperature increase, but it was affected by extreme temperatures, being lower at 10–20°C (6.9 ± 2.3 days) and 25–35°C (6.1 ± 0.6 days). On the other hand, higher female

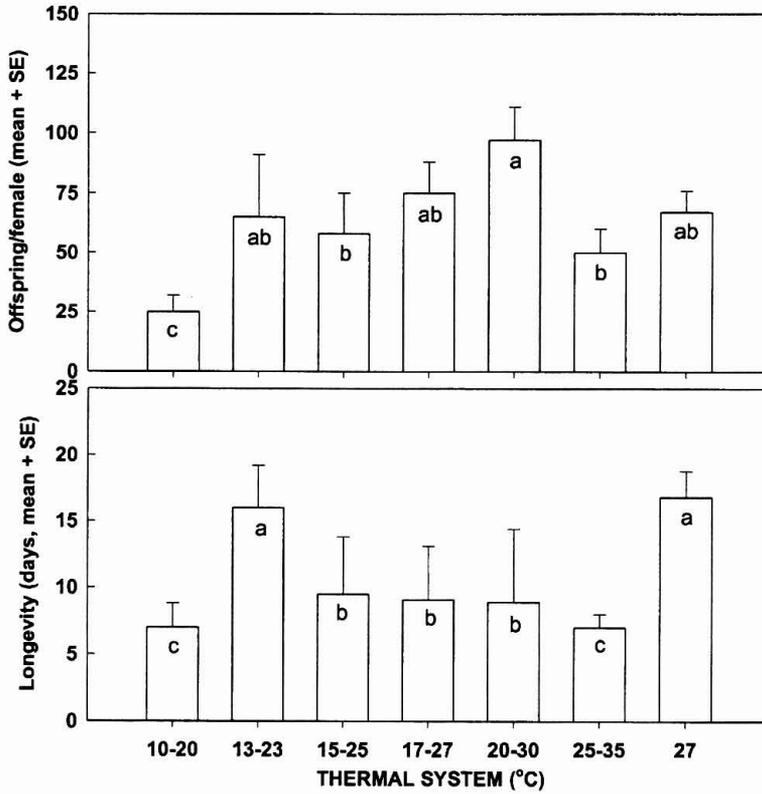


FIGURE 1. Mean number (\pm SE) of offspring per female and female longevity of *T. brochymenae* reared on *Podisus nigrispinus* eggs in six fluctuating and one constant system temperature.

longevity with less variation (17.6 ± 0.6 days) was recorded at a constant temperature of 27°C (Figure 1).

Adults of *T. brochymenae* emerging at different temperatures showed similar behavior and external body shape with parasitism activity starting immediately after emergence when *P. nigrispinus* egg batches were offered. Although fecundity increased with temperature, the extreme values of temperature during winter and summer significantly reduced parasitism (Figure 1).

Number of Generations Under Field Fluctuating Temperature Conditions

These results showed that *T. brochymenae* is able to develop during all seasons in the three eucalyptus areas. When calculated, based on the data on thermal requirements and thermal responses obtained in the laboratory, the number of generations ranged from 1.1 to 2.5 per month at Refloralje, while in the CAF and Pains areas it ranged from 1.5 to 2.5 and 1.5 to 2.4 generations per month, respectively (Figure 2). The employment of two thermal systems, i.e. constant and fluctuating temperatures, did not influence the estimated total number of generations per year of *T. brochymenae* at CAF, Pains and Refloralje. However, there were significant differences among areas ($F = 10.04$; $df = 2, 27$; $P < 0.001$) under constant as well as under fluctuating temperatures ($F = 8.87$; $df = 2, 27$; $P < 0.01$). A lower number of generations of *T. brochymenae* per year at constant and fluctuating temperatures (23.6 and 23.0) were estimated to occur under Refloralje conditions than in CAF and Pains areas. Under estimated conditions for these last two areas, *T. brochymenae* produces similar

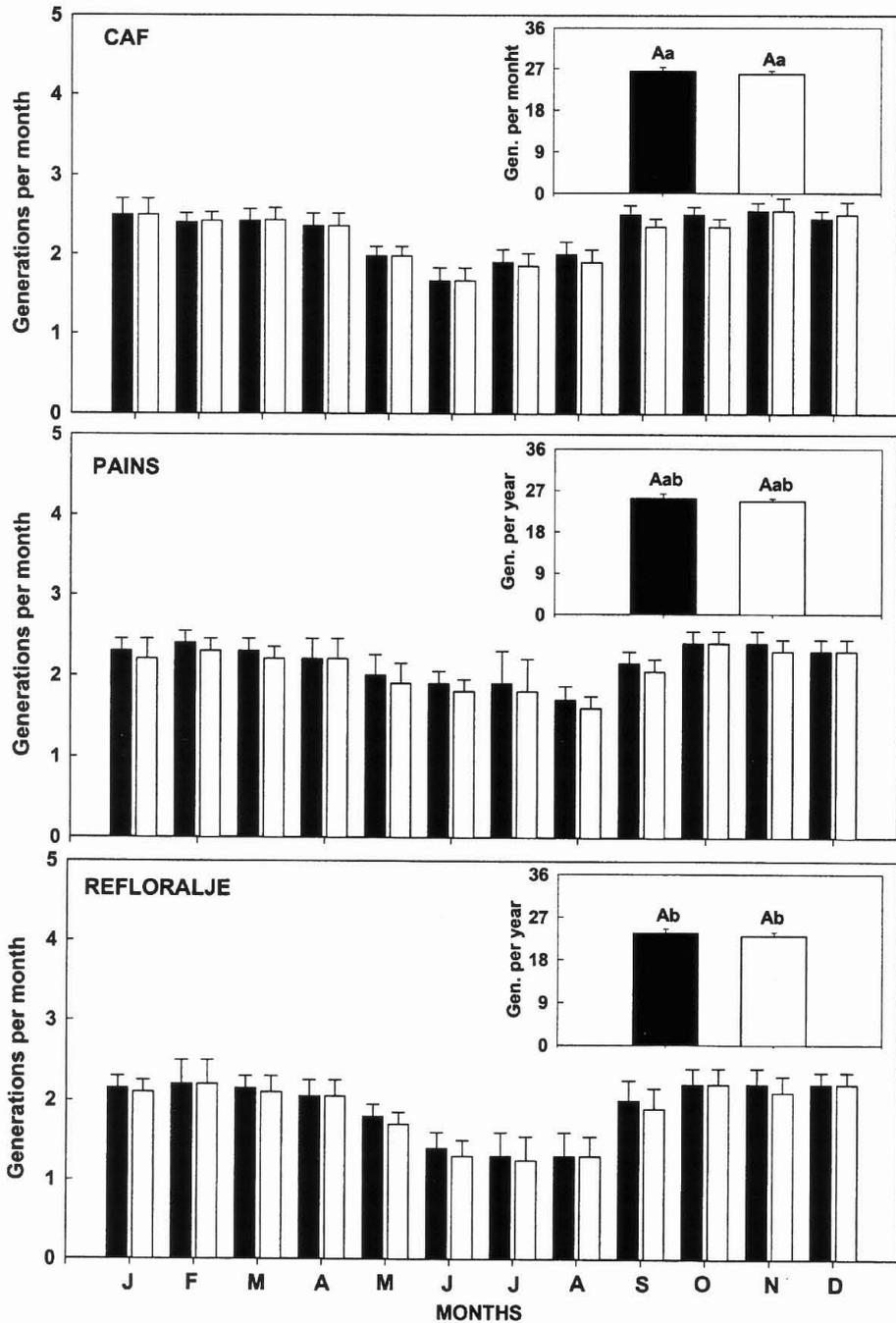


FIGURE 2. Mean number (\pm SE) of generations of *T. brochymenae* estimated per month and year based on constant (filled bars) and fluctuating (open bars) field temperatures summarized from three areas CAF, Pains and Refloralje where the stinkbug predator is released for *Eucalyptus* defoliator control. (Bars having an identical small letter designating generations per year, among areas at constant or fluctuating temperatures or capital letters between thermal systems within the same area are not significantly different at the 0.05 level by Tukey test).

number of generations per year (CAF, 26.4 and 25.8; Pains, 25.3 and 24.7) (Figure 2). The mean temperature variation throughout the year at the Refloralje area shows a marked decrease from May to August, and a similar decrease is observed for the number of generations; while less variation in number of generations throughout the year is depicted in Figure 2 for other areas.

DISCUSSION

A direct influence of temperature on developmental rate has been reported (within a limited range of constant temperatures) for several species of *Trissolcus* when using several pentatomid pests rather than predatory pentatomid species as hosts (Yeorgan, 1980; Orr *et al.*, 1985; James & Warren, 1991; Corrêa-Ferreira & Moscardi, 1994; Cividanes & Figueiredo, 1996). However, the shorter developmental period of *T. brochymenae* at constant or fluctuating temperatures when reared on *P. nigrispinus* indicates that this stinkbug predator is a suitable host for this parasitoid. Cividanes and Figueiredo (1996) reported that the developmental period of *T. brochymenae* on *P. guildinii* at constant temperatures of 27 and 30°C was 14.8 ± 9.2 and 12.8 ± 0.2 days, respectively, with no significant difference between sexes. In our study with *P. nigrispinus* as a host, the developmental period in both thermal systems was shorter in both females and males as well as with smaller variation (Table 1). Emergence rate was also higher in our experiments than that reported by Cividanes and Figueiredo (1996) on eggs of *P. guildinii* (38.6%) at a constant temperature of 30°C. This suggests a higher food utilization and assimilation by *T. brochymenae* as a result of better metabolic activity process on this host.

Other egg parasitoids in the genera *Trissolcus* and *Telenomus* have been often reported on predatory stinkbug such as *Podisus maculiventris* (Say) (Yeorgan, 1979; Buschman & Whitcomb, 1980), *P. nigrispinus* and *P. sculptus* (Torres *et al.*, 1996a; Zanuncio *et al.*, 2000). In addition, *Telenomus podisi* Ashmead has been caught in *P. maculiventris* pheromone traps in numbers related to the predator population after overwintering periods (Aldrich *et al.*, 1984). Similarly *T. brochymenae* has shown a population increase related to *Podisus* spp. populations released in eucalyptus plantations (Torres *et al.*, 1996a; 2001; Zanuncio *et al.*, 2000).

Trissolcus brochymenae performed better at fluctuating temperatures than did *T. podisi*, because the latter showed lower survival at 17 and 32°C, whereas *T. brochymenae* was not negatively affected by these temperatures (Torres *et al.*, 1997). The development of *T. brochymenae* at lower temperatures on *P. nigrispinus* shows that this parasitoid is better adapted to greater temperature fluctuations and to this host than *T. podisi*. Generally, the oviposition rate reaches a maximum at relatively high temperatures near to the upper limit for egg hatching, falling sharply above this maximum, but more gradually below it. Thus, our results indicate that, under field conditions, the parasitism rate by *T. brochymenae* is four times larger during a period of favorable spring-summer temperatures (96 offspring per female) than during the winter season (24 offspring per female) (Figure 1). Also, a negative effect can be hypothesized for egg-adult developmental period and reproduction of *T. brochymenae* when high (sub-optimal) temperatures prevail during the summer.

Sex ratio, emergence rate and threshold temperatures of *T. brochymenae* were not affected by fluctuating temperatures (Table 1), possibly because the fluctuating temperature regime used for the summer (25–35°C, mean = 30.83°C) and winter (10–20°C, mean = 15.83°C) series did not provide average upper and lower temperature levels exceeding threshold temperatures for both predator host and parasitoid development (i.e. 35°C for *P. nigrispinus*, Torres *et al.*, 1998; and 32°C for *T. brochymenae*, Torres *et al.*, 1997). On the other hand, the temperature variations within upper and lower thresholds can affect development and female offspring production for predator and parasitoid (Didonet *et al.*, 1995; 1996; Torres *et al.*, 1997; 1998). Females of *T. brochymenae* tend to produce the same proportion of males throughout their lifetime, producing 20–30% male offspring from the first egg batch parasitized and maintaining this percentage up to the last egg batch parasitized. Variation

in sex ratio was observed in a related species *Trissolcus basalis* (Wollaston) when prior parasitism by a conspecific wasp occurred or when wasps attacked egg masses of different sizes and at different encounter rates (Colazza, 1993). Thus it might be supposed that sex ratio variation was not recorded in our study because females were allowed to oviposit on egg mass of the same size and during a fixed time.

Although females of *T. brochymenae* showed similar sums of degree-days for development in both thermal systems (constant = 214.7 and fluctuating = 213.2), males had smaller sums than females due to their shorter egg-adult period. However, males reared at fluctuating temperatures were more sensitive to temperature variation. The shorter time required by the egg parasitoid to complete egg-adult development in relation to that of the stinkbug host *P. nigrispinus* (parasitoid ~23 to 26, based on Table 2; and stinkbug predator 10 generations per year, based on Didonet *et al.*, 1996), is a factor that allows this parasitoid to reach a high parasitism rate at the end of caterpillar outbreaks in eucalyptus forest and in soybean crops (Corrêa-Ferreira & Moscardi, 1995; Torres *et al.*, 1996a). Thus, regarding the season/month when the number of degree-days reached a predetermined heat accumulation for a rapid development for both parasitoid and host; the parasitoid went through twice as many generations as the stinkbug predator, which depending on the season, had only 0.6 to 1.1 generations per month.

The results obtained can be used to determine the months when the egg parasitoid is likely to colonize and increase its population (Figure 2). A continuous assessment of caterpillar outbreaks in these studied areas is performed by the forestry companies through an adult monitoring program, which designates susceptible eucalypt plots and the timing of attacks (Zanuncio *et al.*, 1994b, 1996). These data are used to focus predator releases. Based on the parasitoid development presented here, decisions on when to initiate stinkbug predator releases and to determine the interval between them can be made, and the time required for the parasitoid to become established in those areas estimated (Torres *et al.*, 1996a). Thus, the companies are able to establish a schedule of stinkbug predator release which avoids high parasitoid impact, as suggested by Torres *et al.* (1996a). For instance, from May to August in the Refloralje area, *T. brochymenae* achieved an average of 1.2 generations per month (Figure 2) while the stinkbug predator reached ~0.3 generations, so, in the following months the parasitoid can become a strong factor for suppressing the stinkbug predator population. This is supported by the observations of Torres *et al.* (1996a), the reported 27.5% parasitism of stinkbug predator eggs in a monitored area of 125 hectares of *Eucalyptus cloeziana* with continuous releases of this predator, while in areas with initial and programmed releases parasitism reached a maximum of only 8.8% at 73 days after releasing. Also, RH affects nymphal hatching of the stinkbug predator and parasitoid emergence, because pentatomid egg hatching is directly affected when RH falls below 50%, reaching zero at 25% RH (Javahery, 1994). Thus, more accurate results of this host-parasitoid association will only be achieved when not only temperature but also other environmental factors are taken into consideration. Besides, it is necessary to determine parasitoid impact on its host in field conditions, which may be affected by biotic and abiotic factors in the forest ecosystem. In conclusion, fluctuating thermal conditions can yield more realistic models for *T. brochymenae* under field conditions, especially when the fluctuating temperatures include those lower than the optimum (from 20 to 30°C). For example, at simulated fluctuating winter temperatures (13–23°C), parasitism was similar to that achieved at a constant temperature of 27°C.

ACKNOWLEDGEMENTS

We thank Professor Carl W. Schaefer, University of Connecticut, USA, for comments on an early draft of the manuscript and to Marcia G. Goes for helping in the maintenance of parasitoid colonies. This research was, in part, supported by CAPES.

REFERENCES

- ALDRICH, J.R., KOCHANSKY, J.P. & ABRAMS, A.C. (1984) Attractant for a beneficial insect and its parasitoid: Pheromone of the predatory spined soldier bug, *Podisus maculiventris* (Hemiptera: Pentatomidae). *Environmental Entomology* **13**, 1031–1036.
- BARCELOS, J.A., ZANUNCIO, J.C., OLIVEIRA, A.C. & NASCIMENTO, E. (1994) Performance em duas dietas e descrição dos adultos de *Brontocoris tabidus* (Signoret) (Heteroptera: Pentatomidae). *Anais da Sociedade Entomológica do Brasil* **23**, 519–524.
- BUSCHMAN, L.L. & WHITCOMB, W.H. (1980) Parasites of *Nezara viridula* (Hemiptera: Pentatomidae) and other Hemiptera in Florida. *Florida Entomologist* **63**, 154–162.
- CIVIDANES, F.J. & FIGUEIREDO, J.G. (1996) Desenvolvimento e emergência de *Trissolcus brochymenae* (Ashmead) e *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae) em diferentes temperaturas. *Anais da Sociedade Entomológica do Brasil* **25**, 207–211.
- COLAZZA, S. (1993) Factors influencing brood sex ratio in the egg parasitoid *Trissolcus basalis* (Woll.) (Hymenoptera: Scelionidae). *Entomologica* **27**, 211–219.
- CORRÊA-FERREIRA, B.S. & MOSCARDI, F. (1994) Temperature effect on the biology and reproductive performance of the egg parasitoid *Trissolcus basalis* (Woll.). *Anais da Sociedade Entomológica do Brasil* **23**, 399–408.
- CORRÊA-FERREIRA, B. S. & MOSCARDI, F. (1995) Seasonal occurrence and host spectrum of egg parasitoids associated with soybean stinkbugs. *Biological Control* **5**, 196–202.
- DIDONET, J., ZANUNCIO, J.C., SEDIYAMA, C.S. & PÍCANÇO, M.C. (1995) Desenvolvimento e sobrevivência ninfal de *Podisus nigrispinus* (Dallas) e de *Supputius cincticeps* Stål (Heteroptera, Pentatomidae) em diferentes temperaturas. *Revista Brasileira de Zoologia* **12**, 513–518.
- DIDONET, J., ZANUNCIO, J.C., PÍCANÇO, M.C. & SEDIYAMA, C.S. (1996) Determinação das exigências térmicas de *Podisus nigrispinus* (Dallas, 1851) e de *Supputius cincticeps* Stål, 1860 (Heteroptera: Pentatomidae), em condições de laboratório. *Revista Brasileira de Entomologia* **40**, 61–63.
- HIGLEY, L.G., PEDIGO, L.P. & OSTILE, K.R., (1986) DEGDAY: a program for calculation of degree-days, and assumptions behind the degree-day approach. *Environmental Entomology* **15**, 999–1016.
- JAMES, D.G. & WARREN, G.N. (1991). Effect of temperature on development, survival, longevity and fecundity of *Trissolcus oenone* Dodd (Hymenoptera: Scelionidae). *Journal of the Entomological Australian Society* **30**, 303–306.
- JAVAHERY, M. (1994) Development of eggs in some true bugs (Hemiptera: Heteroptera). Part I. Pentatomidae. *The Canadian Entomologist*, **126**, 401–433.
- MILLER, J.C. (1992) Temperature-dependent development of the convergent lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology* **21**, 197–201.
- ORR, D.B., BOETHEL, D.J. & JONES, W.A. (1985) Development and emergence of *Telenomus chloropus* and *Trissolcus basalis* (Hymenoptera: Scelionidae) at various temperatures and relative humidities. *Annals of the Entomological Society of America* **78**, 615–619.
- PETERSON, R.K. & MEYER, S.J. (1994) Relating degree-day accumulations to calendar dates: alfalfa weevil (Coleoptera: Curculionidae) egg hatch in the North Central United States. *Environmental Entomology* **24**, 1404–1407.
- StatSoft. (1995) *StatSoft for Windows: General conventions & statistics I. User's handbook*. Microsoft Corporation, Tulsa.
- TORRES, J. B., ZANUNCIO, J.C., CECON, P.R. & GASPERAZZO, W.L. (1996a) Parasitismo de ovos de *Podisus nigrispinus* (Dallas) em áreas de liberação. *Anais da Sociedade Entomológica do Brasil* **25**, 465–473.
- TORRES, J.B., ZANUNCIO, J.C., PÍCANÇO, M.C. & OLIVEIRA, A.C. (1996b) Parameters poblacionais de tres parasitoides (Hymenoptera: Scelionidae, Encyrtidae) utilizando el depredador *Podisus nigrispinus* (Hemiptera: Pentatomidae). *Revista de Biología Tropical* **40**, 233–240.
- TORRES, J.B., PRATISSOLI, D. & ZANUNCIO, J.C. (1997) Exigências térmicas e potencial de desenvolvimento dos parasitoides *Telenomus podisi* Ashmead e *Trissolcus brochymenae* (Ashmead) em ovos do percevejo predador *Podisus nigrispinus* (Dallas). *Anais da Sociedade Entomológica do Brasil* **26**, 445–453.
- TORRES, J.B., ZANUNCIO, J.B. & OLIVEIRA, H.N. (1998) Nymphal development and adult reproduction of the stinkbug predator *Podisus nigrispinus* (Het.: Pentatomidae) under fluctuating temperatures. *Journal of Applied Entomology* **122**, 509–514.
- TORRES, J.B., ZANUNCIO, J.C. & PRATISSOLI, D. (2001) Egg mortality factors of *Podisus nigrispinus* (Heteroptera: Pentatomidae) in *Eucalyptus cloeziana* plantations. *Naturalia* (in press).
- YEARGAN, K.V. (1979) Parasitism and predation of stinkbug eggs in soybean and alfalfa fields. *Environmental Entomology* **8**, 715–719.
- YEARGAN, K.V. (1980) Effects of temperature on development rate of *Trissolcus euchisti* (Hymenoptera: Scelionidae), a parasite of stinkbug eggs. *Annals of the Entomological Society of America* **75**, 181–183.
- WAGNER, T.L., WU, H.I., SHARPE, P.H.I. SCHOOFIELD, R.M. & COULSON, R.N. (1984) Modeling distributions of insect development time: A literature review and application of the Weibull function. *Annals of the Entomological Society of America* **77**, 457–487.
- ZANUNCIO, J.C., ALVES, J.B., ZANUNCIO, T.V. & GARCIA, J.F. (1994a) Hemipterous predators of eucalypt defoliator caterpillars. *Forest Ecology and Management* **65**, 65–73.

- ZANUNCIO, J.C., NASCIMENTO, E.C., GARCIA, J.F. & ZANUNCIO, T.V. (1994b) Major lepidopterous defoliators of eucalypt in Southeast Brazil. *Forest Ecology and Management* **65**, 53–63.
- ZANUNCIO, J.C., TORRES, J.B. & ZANUNCIO, T.V. (1996) Programa cooperativo para o manejo integrado de pragas florestais. *1st Workshop sobre fitossanidade florestal do Mercosul*. UFSM-CEFET, 1–7.
- ZANUNCIO, J.C., OLIVEIRA, H.N., TORRES, J.B. & ZANUNCIO, J.S. (2000) Egg parasitoids of *Podisus sculptus* Distant (Heteroptera: Pentatomidae) in an *Eucalyptus* plantation in the Brazilian Amazonian region. *International Journal of Tropical Ecology*, **48**, 989–992.