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Mass rearing requirements and ecological zoning of *Telenomus remus* estimated through life table in different temperatures and relative humidities

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HIGHLIGHTS

- *Telenomus remus* K is 210.36 GD, Tt is 10.6 °C and Tmax is 35.9 °C.
- Highest values of net reproduction rate (R_0) were obtained in thermal ranges between 25 and 30 °C.
- Highest values of R_0 were obtained in RH ranges between 50 and 70%.
- Ecological zoning based on R_0 presented Sep. to Feb. as the most suitable period for *T. remus.*
- Ecological zoning based on number of generations showed south region of Brazil as less suitable for *T. remus*.

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ABSTRACT

Spodoptera frugiperda (J.E. Smith) is an important polyphagous pest of corn (maize) crops, reported as invasive on most continents. It is the main corn pest in South America. Control methods involve the use of agrochemicals and genetically modified cultivars. Among the possible alternatives for controlling this species, the present study evaluated the biological development of an isofemale line of *Telenomus remus* Nixon collected in Piracicaba, São Paulo, Brazil, on eggs of *S. frugiperda* at different temperatures and relative humidity (RH) levels. The development and parasitism of the parental generation of *T. remus* and its offspring were evaluated at different temperatures (18, 20, 22, 25, 28, 30, 33, and 35 °C) and RH levels (30, 50, 70, and 90 %). Fertility life tables were constructed based on the values obtained at different temperatures and RH. The estimated thermal constant (K) was 210.36 degree-days, the lower temperature threshold (Tt) 10.6 °C, and the upper developmental threshold (Tmax) 35.9 °C. In both generations, *T. remus* showed the best parasitism performance at temperatures between 25 and 30 °C and RH between 50 and 70 %. We represented the results geographically, producing two types of zoning maps, one based on R_0 (net reproductive rate) values and another based on the number of *T. remus* generations in municipalities according to the calendar for the first and second corn crops. Both zoning approaches indicated that the North, Northeast, Midwest, and Southeast regions of Brazil are the most suitable for the establishment and multiplication of *T. remus*, especially from September to February. In the colder Southern region, conditions are suitable only from November to March. Under the same climate conditions as *S. frugiperda, T. remus* can produce 4 to 6 times more generations in both corn crops. For the first corn crop, more regions of Brazil are favorable for the release of *T. remus* to control *S. frugiperda*.

1. Introduction

The fall armyworm *Spodoptera frugiperda* (J.E. Smith) is a highly important crop pest, although restricted to the Neotropics (Ashley et al., 1989; Clark et al., 2007), standing out for its high biotic potential and polyphagous feeding habits and for attacking economically important crops (Knipling, 1980; Casmuz et al., 2010; Montezano et al., 2018). *Spodoptera frugiperda* gained worldwide notoriety after it was reported

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in countries in Africa, Asia, and Oceania, becoming a threat to the economy and food security in those regions (Goergen et al., 2016; Kenis et al., 2017; Ganiger et al., 2018; Sharanabasappa et al., 2018; Yang et al., 2019; EPPO, 2020; Sun et al., 2021).

Control methods against *S. frugiperda* include the use of agrochemicals and genetically modified plants resistant to lepidopteran pests (Adamczyk and Sumerford, 2001; Bernardi et al., 2014; Fatoretto et al., 2017). However, populations resistant to these control methods have been reported (Storer et al., 2010; Fatoretto et al., 2017). Another pest-control method is the use of natural enemies, including macro- and micro-organisms (DeBach, 1964; Parra et al., 2021a). The wasp *Telenomus remus* Nixon is a parasitoid specific to members of the order Lepidoptera, with *S. frugiperda* as one of its main hosts (Gupta and Pawar, 1985; Cave, 2000). This parasitoid is prominent among other natural enemies because of its high parasitism capacity and ability to parasitize the inner layers of the pest's egg mass (Cave, 2000). In Brazil, *T. remus* has been introduced three times, beginning in the 1980 s. It was first reported as occurring naturally in 2020, when it was found in areas of corn (maize) and soybean cultivation in the states of São Paulo (SP) and Paraná, respectively, in locations approximately 500 km apart (Wengrat et al., 2021).

For adoption of a natural enemy in biological control programs, it is necessary to understand its biological attributes (Parra and Coelho Jr., 2022). For this reason, investigating the effects of temperature and relative humidity (RH) on insects is essential to determine the optimal conditions required for laboratory rearing and field release (Parra, 2010; Garcia et al., 2019). Although certain biological attributes of an introduced line of *T. remus* have been determined in different temperatures and RH (Pomari et al., 2012 and 2014), life-table parameters were not constructed for different temperatures and RH. Estimation of life-table parameters enables a better understanding of rates of population increase. In addition to basic aspects of natural enemies, studies that determine their biological parameters in relation to a range of temperatures and RH levels can be used for ecological zoning (Westbrook et al., 2015; Garcia et al., 2018; Parra et al., 2021b), although the effect of RH is seldom used in insect zoning.

The present study determined the biological parameters of a *T. remus* isoline at different temperatures (18, 20, 22, 25, 28, 30, 33, and 35 °C) and RH levels (30, 50, 70, and 90 %). These data were used to construct fertility life tables and produce a map of ecological zoning in Brazil, based on the R_0 (net reproductive rate) values and the number of generations. This zoning approach will help to identify the most favorable periods for release of the parasitoid in both corn crop seasons.

2. Material and methods

2.1. *Telenomus remus* rearing

The population of *T. remus* used for the experiments was obtained from parasitoids collected in a cornfield in Piracicaba, SP, Brazil (22°41.716′ S and 47°38.478′ W). To maintain the quality of the parasitoids, this *T. remus* isoline was obtained by nine generations of backcrossing (inbreeding process), which theoretically reduced the genetic variability of nuclear DNA to less than 0.01 % and the potential for heterosis to less than 14 % (Coelho Jr et al., 2016; Paula et al., 2023).

The parasitoids were reared on *S. frugiperda* eggs obtained from a laboratory population maintained at the Laboratory of Insect Biology, University of São Paulo (USP)/Luiz de Queiroz College of Agriculture (ESALQ), using an artificial diet based on the method described by Parra (2001).

Previously parasitized egg masses of *S. frugiperda* were placed in 600-mL glass vials sealed with PVC film and kept in a climate-controlled chamber set at 25 ± 1 °C, 70 ± 5 % relative humidity (RH), and a 14-h photoperiod until the parasitoids emerged.

Two days after the parasitoids emerged, pieces of cardboard containing non-parasitized egg masses of *S. frugiperda* were offered inside the glass vials containing the emerged parasitoids. Small drops of pure honey were placed on the edge of the cardboard pieces as a food source for the adult parasitoids. After 48 h of parasitism, the egg masses were removed from the vial and divided into two new containers, which were kept in the same climate-controlled chamber as above.

2.2. *Telenomus remus* thermal requirements

To evaluate the effect of temperature, *T. remus* females (at least 24 h old) were placed individually in glass tubes (8.5 *h* x 2.5 Ø cm) sealed with PVC film. Inside the tube, a droplet of pure honey was provided as food for the female, along with a batch of approximately 200 eggs of *S. frugiperda* for parasitism.

The tubes were kept in climate-controlled chambers at eight different temperatures (18, 20, 22, 25, 28, 30, 33, and 35 ± 1 °C) and RH 70 ± 5 %. For each temperature, 25 females were used individually (repetitions). After 24 h of parasitism, the females were removed from the tubes, and the egg masses were kept inside the sealed glass tubes in their respective climate-controlled chambers where the parasitism occurred. The parasitism and parasitism viability of the parental generation were recorded, based on the numbers of parasitized eggs and eggs with exit holes.

From these egg masses parasitized during a period of 24 h, the egg-adult developmental period of *T. remus* at each temperature was determined, from the day of parasitism until all parasitoids emerged (the range of emergence times was recorded). The number of emerging females and males was recorded daily, to determine the effect of temperature on the *T. remus* sex ratio.

In order to assess the effect of temperature on the offspring (F1) generation, 25 females from the second day of emergence and from each temperature were isolated and kept at the same temperature at which the immature stage developed. Parasitism was evaluated over the entire adult phase of *T. remus.* To assess the parasitism of *S. frugiperda*, egg masses were offered to the females daily and after 1 day were replaced with new egg masses. The parasitized egg masses were placed in individual glass tubes and transferred to climate-controlled chambers set at 25 ± 1 °C, RH 70 ± 10 %, and a 14-h photophase. This process of offering egg masses to *T. remus* females was continued until each female died. The parasitized eggs were transferred to a new chamber and kept in the same conditions as in the parasitism until no further parasitoids emerged. From these egg masses, the total parasitism capacity of *T. remus* was determined by counting the number of parasitized eggs, and the parasitism viability by counting the eggs with exit holes.

The biological parameters evaluated for the parental generation were the number of eggs parasitized in 24 h and the parasitism viability. For the offspring, the duration of the egg-adult period, number of eggs parasitized throughout the female's life span, female longevity, parasitism viability, and sex ratio were evaluated.

The thermal constant (K) expressed by equation (1) in degree-days (DD) and the lower thermal threshold (T_t) were estimated, using a linear model.

$$K = D(T - Tt) \tag{1}$$

The upper developmental threshold (Tmax) was estimated using the Brière model (Brière et al., 1999).

2.3. Hygrometric requirements for the development of *Telenomus remus*

The experiment to evaluate the effect of the relative humidity (RH) level on *T. remus* was conducted similarly to the temperature experiment, with the difference that to optimize humidity exchange between the climate-controlled chamber and the inside of the glass tubes, silicone caps with two layers of voile fabric in the center were used to seal the tubes.

At this stage, four different RH levels (30, 50, 70, and 90 ± 10 %) were evaluated, with a constant temperature set at 25 ± 1 °C and a 14-h photophase. The parameters evaluated were the same as in the temperature experiment.

2.4. Statistical analysis

The data for *T. remus* parasitism in both experiments (items 2.2 and 2.3) were analyzed using generalized linear models (GLM) (Nelder and Wedderburn, 1972) of the quasi-Poisson distribution. The data for parasitism viability and sex ratio were analyzed by quasi-binomial GLM. Goodness-of-fit was assessed using half-normal plots with simulation envelopes for all models, (HNP) function (Moral et al., 2017). The F value was calculated using an ANOVA applied to the GLM. When a significant difference between treatments was observed, multiple comparisons of means were performed (Tukey test, $P < 0.05$), using the general linear hypotheses (GLHT) function from the multcomp package (Hothorn et al., 2008). Parasitoid egg-adult duration and longevity in all experiments were analyzed by using the Kaplan–Meier estimator (Kaplan and Meier, 1958), through the survival package (Therneau, 2015). After significant differences between treatments were identified, the log-rank test was used to compare paired treatment means (Matthews and Farewell, 2007).

2.5. Fertility life table of Telenomus remus at different temperatures and relative humidity levels

Using the data obtained from the above experiments (2.2 and 2.3), parameters for the fertility life table of *T. remus* were determined for eight temperatures and four RH levels. The following parameters were used to construct the fertility life table: female longevity, egg-adult duration, viability of this period, pre-oviposition period, daily parasitism, and sex ratio. The parameters obtained were the net reproduction rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ), and doubling time (TD).

These parameters were calculated following Silveira Neto et al. (1976) and Maia et al. (2000), using the equations:

$$R_0 = \sum mx.lx \tag{2}$$

$$rm = \frac{\ln R_0}{T} \tag{3}$$

$$\lambda = e^{rm} \tag{4}$$

$$T = \frac{\ln R_0}{r_m} \tag{5}$$

$$TD = \frac{\ln 2}{r_m} \tag{6}$$

To construct the table, we considered mx as the number of offspring produced in stage x (age interval in which the sample was taken) and lx as the survival rate in stage x. The value of the mean generation time (T) was calculated to estimate the values of r_m but was not included in the fertility life table. The indices were compared statistically using the Bootstrap test with 10,000 simulations (Maia et al., 2000; Reigada et al., 2018).

2.6. Zoning of Telenomus remus in Brazil based on R_0 at different temperatures and relative humidity levels

The zoning of *T. remus* in *S. frugiperda* eggs in Brazil was carried out based on the functions that relate R_0 (net reproductive rate) to the monthly means of the physical variables (temperature and relative humidity). A Gaussian function G(T) was used for temperature values, and a linear function L(RH) was used for relative humidity values, both related to R_0 values. To generate a 3D function representing R_0 values for both temperature and relative humidity, these functions were combined, according to function (7) (Rodrigues et al., 2023):

$$R_0(T, RH) = G(T) + L(RH) - a(T) - b(RH) \tag{7}$$

The constants a and b were determined, and the elements a(T) and b (RH) are mathematical terms used to normalize the values of temperature and relative humidity on the same scale.

Based on these functions, R_0 values were estimated for 106 georeferenced points distributed throughout Brazil (NASA Power, 2023). The R_0 values were compiled and organized into a shapefile, using the QGIS software (QGIS Development Team, 2022).

The IDW (Inverse Distance Weighting) interpolation method was used, which allows for the estimation of unknown values based on previously known values, resulting in a visual representation of the reproductive rate of *T. remus* in Brazil. A total of 12 maps were projected, corresponding to the monthly means of temperature and relative humidity at the predefined points.

2.7. Ecological zoning of Telenomus remus based on the number of generations in corn-growing areas in Brazil

Using the obtained values of T_t (lower thermal threshold) and K (thermal constant), the number of generations of *T. remus* was calculated for specific regions. For this calculation, the following equation (Arnold, 1959) was used:

$$G = \frac{N_d(T_a - T_t)}{K} \tag{8}$$

In this equation, G represents the number of generations, N_d is the number of days that the crop remains in the field over a one-year period, T_a is the mean temperature of the region, and for the parasitoid, T_t is the lower thermal threshold and K is the thermal constant.

To develop the maps, a computer program developed by Parra et al., (2021b) was used. The program was developed in Visual Basics version 6.0 and is designed to calculate the number of generations of a species in predetermined crop areas, considering the crop calendar. The crop regions were defined based on 230 municipalities in Brazil and their crop calendars (Parra et al., 2021b).

The number of generations was calculated based on equation (8). The program was modified to calculate this for *T. remus*, by adjusting the values of T_t and K to the corresponding values for the parasitoid.

Using the T_t and K values specific to *T. remus* and Nd for regions with two (first and second) corn crops annually, values were generated to

Table 1
Number of eggs parasitized in 24 h and parasitism viability of the parental generation, and sex ratio of *Telenomus remus* isoline parasitizing eggs of *Spodoptera frugiperda* at different temperatures (70 ± 5 % RH; 14-h photophase).

Temperature (°C)	Eggs parasitized in 24 h[1]	Parasitism viability (%)[1]	Sex ratio (%)[1]
18	20.84 ± 4.17 a	99.18 ± 0.33 a	0.66 ± 0.05 a
20	29.8 ± 5.96 ab	99.1 ± 0.36 a	0.79 ± 0.03 ab
22	47.4 ± 9.48b	99.3 ± 0.30 a	0.77 ± 0.04 ac
25	76.12 ± 15.22c	99.6 ± 0.16 a	0.84 ± 0.04b
28	75.00 ± 15c	99.6 ± 0.19 a	0.79 ± 0.04 bc
30	82.4 ± 16.48c	99.4 ± 0.19 a	0.83 ± 0.01 bc
33	36.68 ± 7.34 ab	99.8 ± 0.45 a	0.64 ± 0.04 a
35	41.8 ± 8.26b	99.8 ± 0.39 a	0.70 ± 0.04 ac

[1] Means followed by the same lowercase letter do not differ significantly from each other according to Tukey's test ($P \leq 0.05$).

Table 2
Telenomus remus isoline egg-adult duration, longevity, total parasitism (number of eggs parasitized throughout the female's life span) and parasitism viability of the offspring (F1 generation) that developed in eggs of *Spodoptera frugiperda* in different temperatures (70 ± 10 % RH; 14-h photophase).

Temperature (°C)	Egg-adult duration (days)[2]	Longevity (days)[2]	Total parasitism[1]	Parasitism viability (%)[1]
18	35.18 ± 0.011 a	8.68 ± 1.01 ab	6.32 ± 1.79 a	100.00[3]
20	22.94 ± 0.09b	10.72 ± 1.14 a	59.96 ± 5.75b	99.87 ± 0.08 ab
22	18.62 ± 0.08c	11.08 ± 1.23 a	74.68 ± 9.77 bc	99.89 ± 0.10 ab
25	13.93 ± 0.04 d	7.36 ± 0.82 a	112.6 ± 7.01 cd	99.57 ± 0.16 ab
28	11.2 ± 0.06 e	8.76 ± 1.07 a	135.16 ± 13.88 d	97.43 ± 1.07c
30	10.08 ± 0.02 fh	7.83 ± 0.81 a	136.84 ± 14.54 d	99.94 ± 0.04 a
33	9.31 ± 0.08 g	7.14 ± 0.53b	107.6 ± 9.29 cd	99.00 ± 0.28 ab
35	9.72 ± 0.06 gh	5.6 ± 0.39b	52.16 ± 6.94b	98.70 ± 0.55 bc

[1] Means followed by the same lowercase letter do not differ significantly from each other according to Tukey's test ($P \leq 0.05$).
[2] Means followed by the same lowercase letter do not differ significantly from each other according to the log-rank test ($P \leq 0.05$).
[3] Considering no variance was found for this treatment, it was taken out from the analyses.

create maps representing the number of generations that the parasitoid would produce in these regions, based on the mean temperature during each crop season.

QGIS software (QGIS Development Team, 2022) was utilized to organize the data in the shapefile format and to create the maps. Two maps were created, each representing the number of generations of *T. remus*, one for municipalities cultivating first-crop corn and another for those cultivating second-crop corn.

3. Results

3.1. Thermal requirements for the development of Telenomus remus

Of the eight temperatures studied (18, 20, 22, 25, 28, 30, 33, 35 °C), *T. remus* showed the highest parasitism performance between 25 and 30 °C ($F_{7;\ 192} = 17.018$; $P < 0.01$). The egg-adult period ranged from 35.2 to 9.3 days within the temperature range of 18 to 33 °C ($X^2 = 456$; df = 7; $P < 0.001$), with a tendency toward unsuitability beyond 35 °C, indicated by a numerical increase in duration, likely as an indication of approaching the upper thermal limit or unsuitable thermal conditions (Tables 1 and 2).

Parasitism viability of the parental generation was not influenced by the different temperatures ($F_{7;\ 178} = 1.586$; $P = 0.142$), remaining above 99 % across all temperatures studied.

None of the temperatures resulted in less than 60 % females produced, although production differed with temperature (Table 2) ($F_{7;\ 178} = 6.36$, $P < 0.01$).

Parasitism of the progeny (F1 generation) was highest at temperatures of 25–33 °C ($F_{7;\ 192} = 32.76$; $P < 0.01$), and female longevity was highest at 18–30 °C, decreasing from 33 °C upward ($X^2 = 98$; df = 7, $P < 0.01$). The viability of the offspring generation again was high, above 97 % in all treatments (Table 2) ($F_{6;160} = 12{,}63$; $P < 0.01$).

The coefficient of determination (R^2) obtained from the linear model was 91 % (Fig. 1), the thermal constant (K) was 210.4 degree-days, and the lower thermal limit (T_t) was 10.6 °C.

Using the Brière model (Brière et al., 1999), the maximum temperature for the *T. remus* isoline development was determined to be 35.9 °C.

3.2. Hygrometric requirements for the development of Telenomus remus

For *T. remus* on *S. frugiperda* eggs, few parameters were affected by the different relative humidity (RH) levels. Of the four RH levels, the number of parasitized eggs was lowest at 30 % RH ($F_{3;96} = 23.87$; $P < 0.01$). The duration of the egg-adult period and the sex ratio were not affected by the RH level (Tables 3 and 4) ($X^2 = 5.8$; df = 3; $P = 0.1$). Again, the parasitism viability was consistently above 90 %, indicating that *S. frugiperda* is highly suitable as a host for *T. remus*, even in low humidity ($F_{3;91} = 1.2$; $P = 0.32$).

In the second stage of the experiment, the parasitism potential was

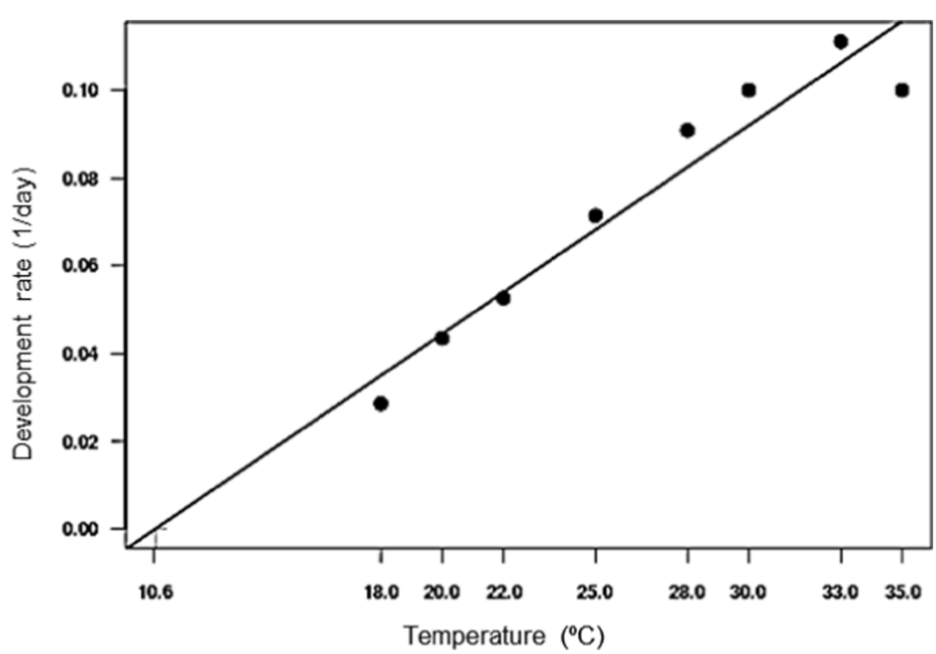

Fig. 1. Development rate of *Telenomus remus* isolate on *Spodoptera frugiperda* eggs at different temperatures (RH 70 ± 10 %; 14-h photophase).

Table 3
Number of eggs parasitized in 24 h and parasitism viability of the parental generation, and sex ratio of *Telenomus remus* isoline parasitizing eggs of *Spodoptera frugiperda* at differen relative humidity levels (25 ± 1 °C; 14-h photophase).

RH (%)	Eggs parasitized in 24 h[1]	Parasitism viability (%)[1]	Sex ratio (%)[1]
30	30.70 ± 6.14 a	99.70 ± 0.56 a	0.66 ± 0.06 a
50	48.12 ± 9.62b	99.90 ± 0.11 a	0.66 ± 0.22 a
70	49.92 ± 10.00b	99.55 ± 0.35 a	0.64 ± 0.26 a
90	57.40 ± 22.32b	99.55 ± 0.32 a	0.74 ± 0.17 a

[1]Means followed by the same lowercase letter do not differ significantly from each other according to the Tukey test ($P \leq 0.05$).
[2]Means followed by the same lowercase letter do not differ significantly from each other according to the log-rank test ($P \leq 0.05$).

Table 4
Telenomus remus egg-adult duration, total parasitism (number of eggs parasitized throughout the female's life span), longevity, and parasitism viability of the offspring (F1 generation) that developed in eggs of *Spodoptera frugiperda* in different humidity levels (25 ± 1 °C; photophase 14 h).

RH (%)	Egg-adult duration (days)[2]	Total parasitism[1]	Longevity (days)[2]	Parasitism viability (%)[1]
30	14.66 ± 0.1 a	43.24 ± 4.09 a	2.00 ± 0.16 a	100.00[3]
50	14.80 ± 0.05 a	145.32 ± 61.07 bc	9.58 ± 0.87b	99.89 ± 0.05 a
70	14.87 ± 0.07 a	165.04 ± 76.35c	11.00 ± 0.93b	99.89 ± 0.04 a
90	14.20 ± 0.48 a	117.4 ± 75.36b	6.28 ± 0.91b	99.81 ± 0.56b

[1] Means followed by the same lowercase letter do not differ significantly from each other according to the log-rank test ($P \leq 0.05$).
[2] Means followed by the same lowercase letter do not differ significantly from each other according to the Tukey test ($P \leq 0.05$).
[3] Considering no variance was found for this treatment, it was taken out from the analyses.

higher at RH levels of 50–90 %, with the lowest values in females that developed at 30 % RH ($F_{3;92} = 3.04$; $P = 0.03$) (Table 4). Thus, the low number of eggs parasitized by females at 30 % RH, which survived for only approximately 2 days, explains the low parasitism in this condition ($X^2 = 75.7$; df = 3; $P < 0.01$).

3.3. Fertility life table of *Telenomus remus* at different temperatures and relative humidity (RH) levels

The parameters obtained from the fertility life table (Table 5) indicated that the values of the net reproductive rate R_0 were higher at temperatures ranging from 22 to 33 °C, indicating the favorable range for the reproductive development of *T. remus*. Temperatures of 18, 20, and 35 °C resulted in lower R_0 values, although the wasps were still able to develop at these temperatures.

The values of r_m (intrinsic rate of increase) and λ (finite rate of increase) for *T. remus* were higher in the range of 25–35 °C, as were the values of TD (doubling time). The parameters obtained from the fertility life table (Table 6) indicated that 30 % RH resulted in lower values for R_0, r_m, and λ, as well as higher values for TD compared to RH levels of 50, 70, and 90 %.

The values of T (mean duration of 1 generation) did not have associated errors, as all repetitions had the same values. The corresponding T values in Tables 1 and 3 correspond to the duration of the egg-adult period.

3.4. Zoning of *Telenomus remus* in Brazil based on R_0 at different temperatures and relative humidity levels

The zoning maps for *T. remus* were constructed based on the values of R_0 obtained from the fertility life tables at different temperatures and relative humidity levels (Tables 5 and 6).

The black and purple areas on the map indicate the best thermo-hygrometric conditions for *T. remus*, suggesting that September to

Table 6
Estimated parameters for the fertility life table of *Telenomus remus* strain on *Spodoptera frugiperda* eggs at four relative humidities (Temperature of 25 ± 1 °C; 14-hour photophase).

RH (%)	R_o^{a1}	r_m^{b1}	λ^{c1}	TD^{d1}
30	27.399b (18.602–37.046)	0.228 a (0.201–0.249)	1.256 a (1.222–1.282)	3.036 a (2.784–3.458)
50	84.239 a (65.575–105.399)	0.3057b (0.288–0.321)	1.357b (1.333–1.378)	2.266b (2.158–2.406)
70	98.901 a (77.610–121.750)	0.3168b (0.299–0.331)	1.372b (1.350–1.393)	2.187b (2.092–2.308)
90	80.889 a (59.366–104.985)	0.3029b (0.281–0.321)	1.353b (1.324–1.377)	2.287b (2.162–2.459)

[a] Net reproduction rate [b] intrinsic rate of increase [c] finite rate of increase [d] population doubling time. Parameters compared by Bootstrap test (10,000 repetitions).
[1] Means followed by the same lowercase letter do not differ significantly.

Table 5
Estimated parameters for the fertility life table of *Telenomus remus* isolate in eggs of *Spodoptera frugiperda* at eight temperatures (RH 70 ± 10 %; photophase 14 h).

Temperature (°C)	R_o^{a1}	r_m^{b1}	λ^{c1}	TD^{d1}
18	4.325c (2.722–5.999)	0.040 a (0.028–0.050)	1.041a (1.028–1.052)	17.007 a (13.733–24.827)
20	47.346 a (33.963–61.870)	0.164b (0.149–0.175)	1.178b (1.162–1.192)	4.222b (3.949–4.629)
22	59.32 5ab (42.452–78.170)	0.209c (0.191–0.224)	1.233c (1.212–1.251)	3.310c (3.098–3.603)
25	85.703b (63.680–109.130)	0.306 d (0.286–0.323)	1.359 d (1.331–1.382)	2.258 d (2.140–2.417)
28	106.101b (76.492–138.069)	0.405 e (0.377–0.429)	1.500 e (1.458–1.535)	1.709 e (1.616–1.835)
30	108.815b (81.587–139.224)	0.446 e (0.418–0.469)	1.563 e (1.520–1.598)	1.552 e (1.474–1.656)
33	64.143 ab (47.856–81.461)	0.438 e (0.408–0.4634)	1.549 e (1.503–1.588)	1.582 e (1.496–1.700)
35	42.195 a (27.607–60.024)	0.356 de (0.316–0.390)	1.371 de (1.371–1.477)	1.944 de (1.776–2.197)

[a] Net reproduction rate, [b] intrinsic rate of increase, [c] finite rate of increase, [d] population doubling time. Parameters compared by Bootstrap test (10,000 repetitions).
[1] Means followed by the same lowercase letter do not differ significantly from each other according to the Bootstrap test.

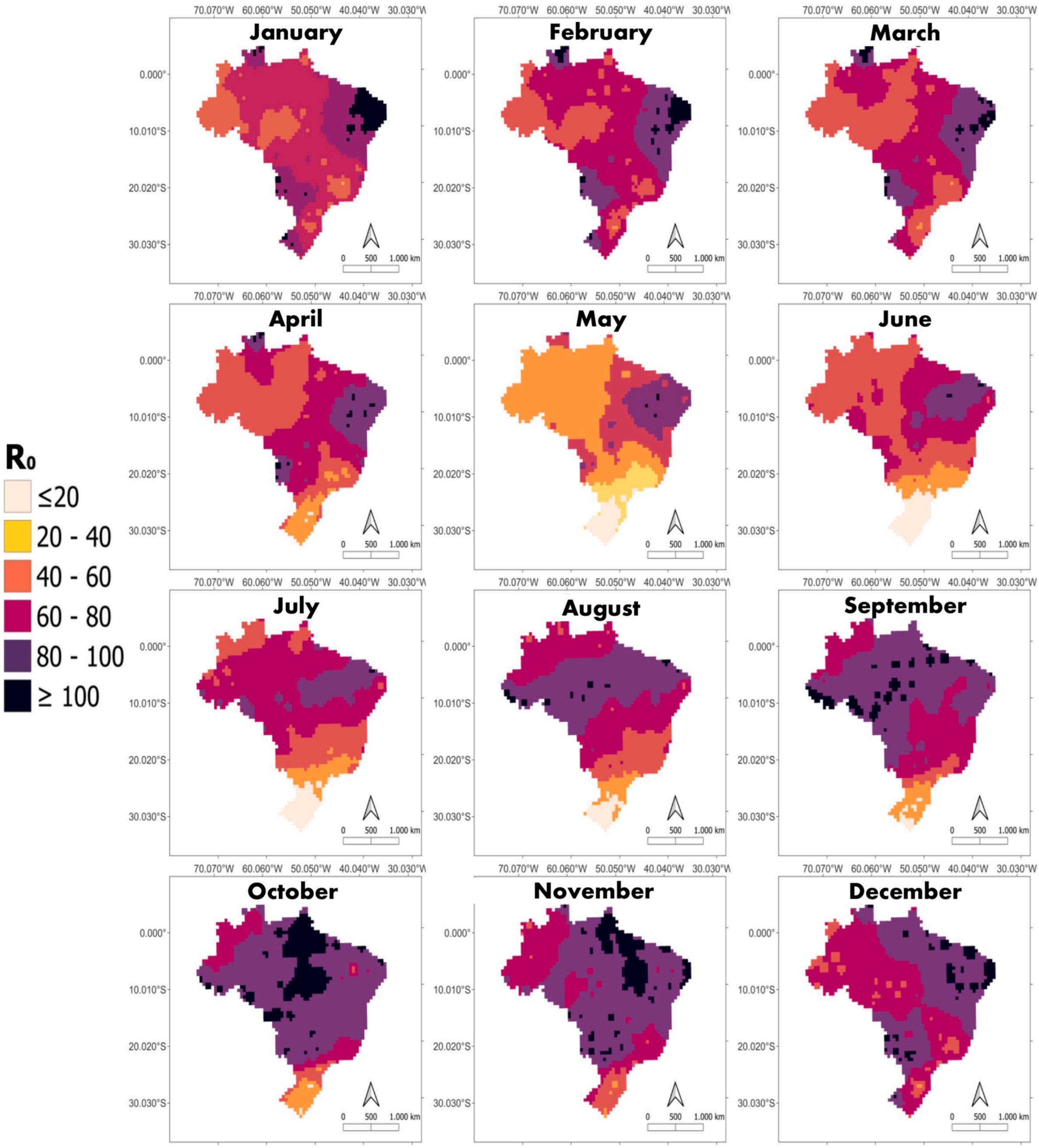

Fig. 2. Interpolated maps showing the monthly distribution of the density of the *Telenomus remus* isoline in Brazil, using the net reproductive rate (R_o) at different temperatures and relative humidity (RH) levels.

February would be the most favorable months for the species. The Southern region is less suitable because of the colder temperatures, but between November and March the climate conditions would allow the parasitoid to reproduce (Fig. 2).

3.5. Ecological zoning of Telenomus remus based on the number of generations in corn-growing areas in Brazil

. There maps enabled an estimate of the potential number of *T. remus* generations for both the first and second crops in the major corn-producing municipalities, taking into account its thermal requirements. *Telenomus remus* can produce from 2.5 to 12 generations in the regions evaluated. The Southern region would support fewer generations than in the North, Northeast, Central-West, and Southeast regions, primarily due to the cooler climate (Figs. 3 and 4).

4. Discussion

The highest parasitism performance of the *T. remus* parental generation occurred in temperatures between 25 and 30 °C. Temperature did

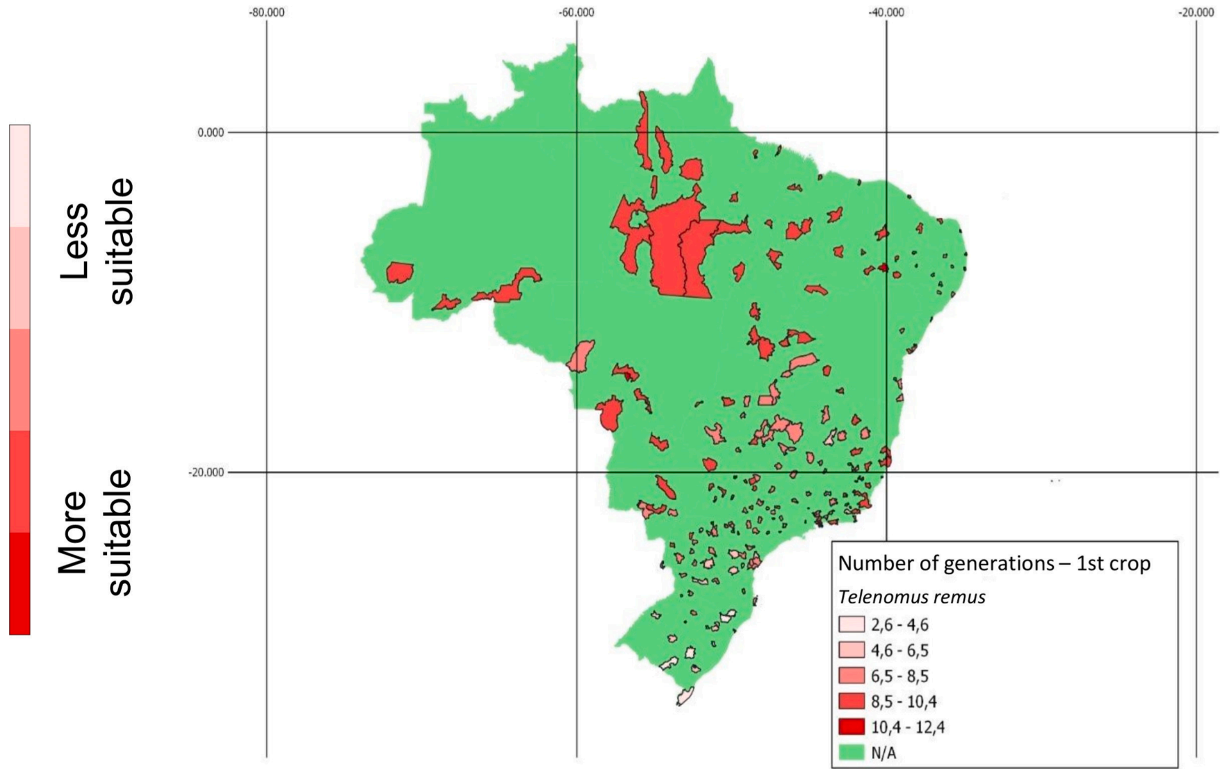

Fig. 3. Map displaying the estimated number of generations per year for the *Telenomus remus* isoline, based on thermal requirements and the regions of first corn crop cultivation.

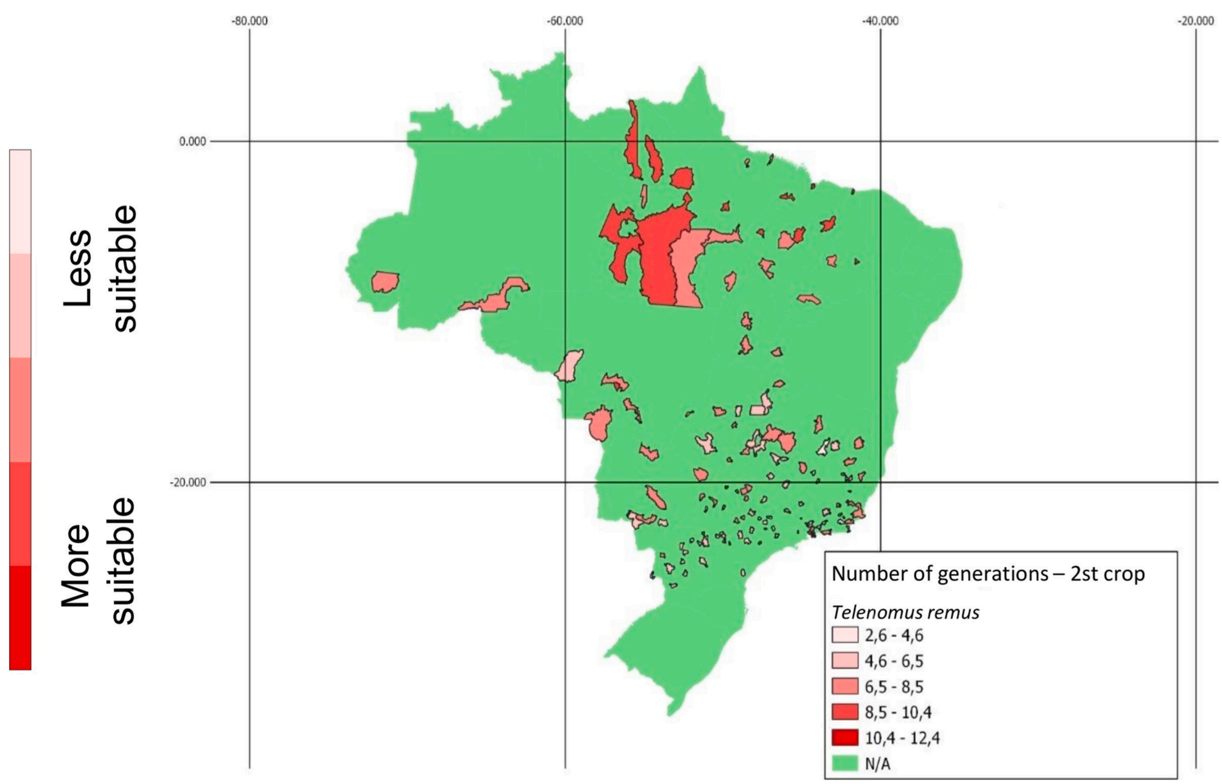

Fig. 4. Map displaying the estimated number of generations per year for the *Telenomus remus* isoline, based on thermal requirements and the regions with a second corn crop.

not influence the parasitism viability of the parental generation. These high viabilities indicate that *S. frugiperda* is highly suitable as a host for *T. remus*, as reported by others (Pomari et al., 2012; Queiroz et al., 2019; Chen et al., 2021; Fortes et al., 2023; Lacerda et al., 2023). The egg-adult period was inversely proportional to temperatures, in the range of 18 to 33 °C. Above 35 °C, the number of days for development increased, likely as an indication of approaching the upper thermal limit or unsuitable thermal conditions. In all temperatures evaluated, at least 60 % females were produced. Production of larger numbers of females is desirable in biological control programs, as females are responsible for parasitism (Navarro, 1998; Bueno et al., 2008).

Parasitism of the progeny (F1 generation) was highest at temperatures between 25–33 °C. Temperatures above 30 °C are probably not suitable for *T. remus* because of the effect on longevity. The viability of the offspring generation was again higher, above 97 % in all treatments.

The thermal requirement values determined here are useful for planning the logistics of mass production of the natural enemy in biofactories or in populations used for research, as these data allow for estimating and scheduling the emergence of the parasitoids and selecting the optimal temperature conditions for the species.

The maximum temperature tolerated by the *T. remus* isoline was determined as 35.9 °C, which differs from the values reported by Bueno et al. (2008) and Pomari et al. (2012). The T_t value obtained was lower than the values reported in those studies. This difference in values could be related to the origin of the parasitoid populations used by Bueno et al. (2008) and Pomari et al. (2012), which originated from Venezuela and were kept in laboratory rearing conditions for more than 10 years (Wengrat et al., 2021). In the present experiment (item 2.1), an isoline of *T. remus* collected in Piracicaba (22°41.716′ S and 47°38.478′ W) in the year 2019 was used (Paula et al., 2023).

Regarding relative humidity (RH), *T. remus* was affected, especially at low relativity humidity levels. Van Welzen and Waage (1987) reported that *T. remus* parasitized the maximum number of eggs on days 1–3, and Pomari et al. (2014) observed that 80 % of *T. remus* parasitism occurred within the first 5 days of the parasitoid's life span. Thus, the low number of eggs parasitized by females at 30 % RH, which survived for only approximately 2 days, explains the low parasitism in this condition.

The parameters from the fertility life table indicated that the values of the net reproductive rate R_0 were higher at temperatures ranging from 22 to 33 °C, which was the favorable range for the development of *T. remus*. Temperatures of 18, 20, and 35 °C resulted in lower R_0 values, although the wasps were still able to develop at these temperatures.

The values of r_m (intrinsic rate of increase) and λ (finite rate of increase) for *T. remus* were highest in the temperature range of 25–35 °C, as were the values of TD (doubling time). The parameters obtained from the fertility life table indicated that 30 % RH resulted in lower values for R_0, r_m, and λ, as well as higher values for TD compared to RH levels of 50, 70, and 90 %. The values of T (mean duration of 1 generation) did not have associated errors, as all repetitions had the same values. The corresponding T values in Tables 1 and 3 correspond to the duration of the egg-adult period.

Using the R_0 values from the *T. remus* life table, we constructed the zoning maps based on different temperatures and relative humidity. Studies that perform zoning for insect pests or natural enemies typically use the number of generations and temperature values to estimate the insect distribution (Lacerda et al., 2019; Rodrigues et al., 2023). The decision to employ R_0 values was motivated by their capacity to increase the precision of quantifying population growth dynamics for a given species, incorporating considerations of fertility and survival rates. Consequently, this approach allows a more accurate estimation of the optimal geographic areas for *T. remus* occurrence in Brazil.

The maps helped to identify areas that are more favorable for the reproductive success of the parasitoid, considering the influence of abiotic factors on the net reproductive rate. At first glance, based only on the results of the thermal-requirement experiments and considering the country of origin of *T. remus*, it appears that this species prefers regions with predominantly high temperatures, above 25 °C, and with high relative humidity, above 50 %. This differs from conditions in São José dos Pinhais where the species has been reported (Wengrat et al., 2021). Its presence there may be due to the selection of strains adapted to adverse temperature and humidity conditions (Pak et al., 1989). Another important aspect is that the results presented in the maps (Fig. 2) use monthly mean values of temperature and relative humidity, providing a macroclimate view. These values do not represent the actual climate variations or microclimate data.

Another zoning approach employed in this study involved the creation of maps that encompassed the areas and periods of the first and second corn crops. Considering the importance of the pest *S. frugiperda*, the present study determined both the reproductive capacity (R_0) of an isoline of the natural enemy *T. remus*, visually represented on a broad (continental) landscape, Brazil, using a range of temperatures and humidity levels combined. The study also estimated the potential number of *T. remus* generations according to the corn-growing season (Parra et al., 2021b). As presented by Garcia et al. (2019), using an index based on Fuzzy Logic, the interaction between an insect pest and its natural enemy is critical for the success of a biological control program. Here we present tools, using the *T. remus* zoning and distribution maps, based on biological data and the crop calendar, that can indicate the best period and locations with the most suitable climate conditions to release the natural enemy. The use of GIS tools based on the extensive data presented here may help to understand the bioecological potential of *T. remus* in a continental-scale landscape, which could guide IPM programs or, preferably, AW-IPM programs (Hendrichs et al., 2021) worldwide, once all needed data are available. Although the zoning methods employed here, based on the biology of the insect, are helpful for a better understanding of *T. remus* dispersal and distribution, improving biological control programs using this parasitoid, one limitation must be addressed. The experiments were performed under laboratory conditions; therefore, these maps, as well as our assumptions, need to be verified in field studies. Model validation is an important step in the modeling process (Garcia et al., 2019), and we are aware that other variables such as rainfall and atmospheric pressure may affect the distribution and number of generations of each species.

CRediT authorship contribution statement

Marília Corrêa de Melo: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Aloisio Coelho:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Adriano Gomes Garcia:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José Roberto Postali Parra:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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