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Life history data and population growth of *Tuta absoluta* at constant and alternating temperatures on two tomato lines

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Abstract

The tomato borer *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), is of growing concern worldwide as a key pest of tomato. In Brazil, the pest is controlled by frequent pesticide sprays, leading to quick development of pesticide resistance in the pest, to high pesticide residue levels on the fruit and to decimation of natural enemies of this and other tomato pests. In order to develop biological control programs, basic information on the biology of the pest *T. absoluta* is essential. In addition, potential occurrence of resistance to the pest in tomato lines might be an interesting option for control of the pest, either alone or in combination with biological control. Therefore, we studied development, sex ratio, weight, fecundity and population growth of *T. absoluta* at constant (25 °C) and alternating temperature (30/20 °C) on two tomato lines (Bravo and Tex 317), which were expected to have different levels of resistance to the tomato borer. Tomato line and temperature regime significantly influenced many life history parameters. Development time was generally shorter and emergence rates higher on Bravo than on Tex 317. However, egg development time was similar on both tomato lines and temperature regimes, though egg survival was much lower on Tex 317. Also larval survival was lower on Tex 317, and this lower egg and larval survival suggests antibiosis resistance. Interestingly, the sex ratio was more female biased at the alternating than at the constant temperature on both tomato lines. Another temperature effect was a longer egg to adult development time on both lines at the alternating temperature regime. The net reproductive rate (R_0) and the intrinsic rate of population increase (r_m) were higher on Bravo than on Tex 317, again indicating that Bravo is the most suitable host plant of the two. On the partially resistant tomato line Tex 317 population development is estimated to be much slower than on line Bravo. Also, *T. absoluta* larvae are exposed longer to natural enemies on Tex 317. Possibilities for biological control of this pest are discussed.

Key words: life table, host-plant resistance, antibiosis resistance, biological control, intrinsic rate of population increase, acyl sugars.

Introduction

The tomato borer *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), a key pest of tomato and native to the western part of South America, invaded Brazil around 1980 (Souza and Reis, 1992). It is now a devastating pest in tomato crops in South America, Europe, Africa and Asia (Tropea *et al*., 2012; Zappalà *et al*., 2013). In most countries where *T. absoluta* occurs, the main control strategy consists of frequent sprays with chemical insecticides, because without control *T. absoluta* causes yield losses up to 100% and dramatically decreases fruit quality in both field and in greenhouse tomato crops (Gilardón *et al*., 2001; Tropea *et al*., 2012). Several species of parasitoids have been tested for control of the tomato borer in Latin America, but reliable and efficient biological control programs are not yet available (Bueno *et al*., 2013). The egg parasitoid *Trichogramma pretiosum* Riley (Hymenoptera Trichogrammatidae) was released to control *T. absoluta* in Brazil (Haji *et al*., 2002) and Colombia (García Roa, 1989), but appeared to provide insufficient pest reduction. In Colombia the larval parasitoid *Apanteles gelechiidivoris* Marsh (Hymenoptera Braconidae) (Bajonero *et al*., 2008) has been tested, but these tests have not yet resulted in commercial application. The larval parasitoids *Pseudoapanteles dignus* (Muesebeck) (Hymenoptera Braconidae) and *Dineulophus phthorimaeae* De Santis (Hymenoptera Eulophidae) are currently evaluated as biological control agents of *T. absoluta* in Argentina (Sánchez *et al*., 2009).

Also in Europe control of the tomato borer heavily relied on insecticides initially. But it soon appeared that two native mirid predators, *Nesidiocoris tenuis* (Reuter) and *Macrolophus pygmaeus* (Rambur), used to control whiteflies and thrips, were very efficient in controlling *T. absoluta* as well and biological control is now generally applied to control this pest (Urbaneja *et al*., 2012; van Lenteren, 2012, Mollà *et al*., 2014).

Based on this European success, we decided to develop a biological control project for the tomato borer using Brazilian heteropteran predators (Bueno *et al*., 2013). In order to do so, we needed to have basic biological data about the biology of *T. absoluta*, but until now very limited information is available (Duarte *et al*., 2015). The pest is multivoltine and the population growth parameters suggest that it is an *r* strategist (Pereyra and Sánchez, 2006). The duration of the life cycle depends on environmental conditions, in particular temperature, and ranges from 76.3 days at 14 °C to 23.8 days at 27 °C (Barrientos *et al*., 1998). Overlapping generations generally occur and all developmental stages are found simultaneously under field conditions (Souza and Reis, 1992).

Due to the presence of *T. absoluta* and a high number of other tomato pests in Brazil (Bueno *et al*., 2013), and because of the warm climate causing a fast development of pest populations, a high frequency of insecticide sprays is needed to be able to harvest tomatoes. Insecticides are sprayed up to 5 times per week and 36 times per tomato production cycle of 12 weeks (Guedes and Picanço, 2012). Tomato is currently the crop with the highest rate of pesticide consumption among the vegetables in Brazil, with an application volume of 54.9 kg active ingredients per production cycle (Agrianual, 2011). As a result, also in Brazil development of resistance to insecticides is usually fast (Haddi *et al*., 2012; Gontijo *et al*., 2013; Campos *et al*., 2015), making them ineffective, while at the same time decimating natural enemy species of the various pests, as well as causing high pesticide residue levels on the harvested tomato fruits (Agrianual, 2011; Guedes and Picanço, 2012). Therefore, a search for alternatives to chemical pesticides is of high priority. We started a project for exploration and evaluation of natural enemies of *T. absoluta* summarized in Bueno *et al*. (2013), as well as to look for the potential to use tomato cultivars that might be resistant or tolerant to this pest, which we report in this paper.

Development of tomato cultivars with resistance to pests is an important strategy in pest control and it is one of the fundamental pillars of integrated pest management (Giustolin *et al*., 2002), which contributes to reduction of pest population densities and might be combined with biological control. Maciel *et al*. (2011) evaluated tomato hybrids for non-preference or antixenosis resistance to *T. absoluta* starting from a Tom-687 lineage rich in acyl sugars. However, non-preference was not found in these hybrids, but they did not test for antibiosis resistance. Expression of resistance is influenced by the physiological state of the host plant and its morphology (Bethke e*t al*., 1998) and expression can be also affected by temperature changes (Kocourek *et al*., 1994). Variations in temperature directly influence the development rate of insects and indirectly influences their development through effects on the host plant, and thus, the plant's quality as food resource (Beck, 1983; Pigliucci, 2005; Karban and Baldwin, 2007). Next, the population growth of an insect depends on the food quality and other environmental influences than temperature (Hagen *et al*., 1984). Understanding how the intrinsic rate of increase varies in relation to these factors (Southwood, 1978; Townsend *et al*., 2006) can assist in the design of control programs for *T. absoluta*.

In this paper, we report about the development, fecundity and population growth of *T. absoluta* under constant and alternating temperature regimes on tomato lines expected to have different levels of resistance to the pest. Also possibilities for biological control of this pest are discussed.

Materials and methods

Experiments were carried out in climate rooms with constant (25 °C) or alternating (day-night: 30/20 °C) temperatures, RH 70 ± 10% and 12 h photophase. Tomato lines Bravo and Tex 317 (both from the Santa Cruz Group, Brazil) were chosen as they were expected to have different levels of resistance to the tomato borer; we use the word line instead of cultivar as these two tomato accessions are still pre-commercial. Line Bravo has a low acyl sugar content, while the pre-commercial line Tex 317 has a high acyl sugar content and a presumed range of resistance to several insect pests (Maciel *et al*., 2011). Tomato plants were cultivated in greenhouses in pots containing sterilized and fertilized soil. Plants in the vegetative stage with 4-5 completely developed leaves were used in the experiments. The experiment consisted of four treatments: two tomato lines and two temperature regimes.

Eggs, larvae and pupae of *T. absoluta* were collected on tomato crops in the field in the municipality of Lavras, Minas Gerais, Brazil, located at 21°14'S 45°00'W and 918 m a.s.l., and kept in the laboratory until adult emergence. Adults were used to start two populations: one on line Bravo and another on Tex 317. Individuals from these populations were used in the experiments.

Egg development and survival

T. absoluta was reared for one generation on each tomato line, and eggs laid by females from the 2nd generation were used in the experiments. Ten *T. absoluta* couples were individually placed in transparent acrylic cups (6.5 cm of height, 8.0 cm of diameter) positioned upside down on a Petri dish (⌀ 10 cm) with either Bravo or Tex 317 leaflets with their petioles inserted in an Eppendorf tube with distilled water and fixed in Styrofoam. The leaflets were used as oviposition substrate. Two honey droplets were added in the cup as food. The couples were kept in the acrylic cup to oviposit for 24 h. Next, the eggs laid on the leaflets were counted under a stereomicroscope, and the number of eggs was reduced to 10 per leaflet. These leaflets were then kept in Petri dishes (⌀ 9 cm) sealed with PVC film, and containing a disc of filter paper to absorb excess moisture. Newly-emerged larvae were counted daily. Egg development time and egg survival were recorded. Ten replicates involving a total of 100 eggs were carried out for both Bravo and Tex 317 at 25 °C and 30/20 °C.

Larval development and survival

Tomato leaflets with the petioles wrapped in moistened cotton were put in Petri dishes (⌀ 9 cm) on a layer of filter paper discs to absorb excess moisture and sealed with PVC film. Twenty-four h old *T. absoluta* eggs were put on each leaflet with the aid of a fine brush and a histological needle under a stereomicroscope (Bogorni and Carvalho, 2006). Each Petri dish with the leaflets was considered a sampling unit and a total of 20 Petri dishes per tomato line and per temperature were evaluated. To determine larval survival, larvae from 5 Petri dishes (n = 100) per treatment were daily observed until pupation. From the remaining Petri dishes (15 Petri dishes and a total of 300 larvae at the start of the experiment for each treatment), one larva per Petri dish was removed daily from the mines in the leaflets with the aid of a fine-tipped stylus, killed in hot water and placed in a plastic tube with 70% alcohol. Of these larvae, the cephalic capsule was measured with a graduated ocular scale (10 mm/100) of a stereomicroscope, to determine the duration of instars with the methodology of Giustolin *et al*. (2002).

Pupal weight and sex ratio

Newly-formed pupae were weighed and sexed as described by Coelho and França (1987). Ten female and ten male pupae were weighed. Also, the sex ratio of 50 pupae was determined. Pupae were then put individually in glass tubes (8.5 × 2.5 cm) until adult emergence.

Reproduction

A tomato leaflet with the petiole inserted into an Ependorf tube, filled with distilled water and fixed in polystyrene was kept in a Petri dish (⌀ 10 cm). This leaflet was used as oviposition substrate for *T. absoluta.* A male and female adult of *T. absoluta* (15 couples/treatment) of one day old coming from larvae developed on the two tomato lines and at the two temperature regimes was placed on the leaflet and the Petri dish was closed by a transparent acrylic cup (6.5 cm, 8.0 cm in diameter). In the upper region of the cup two drops of honey were added as food. The cups as well as the leaflets were changed daily. The number of eggs laid was counted daily under a stereomicroscope. Also, the pre-oviposition, oviposition and post-oviposition period and adult longevity were recorded.

Table 1. Egg development (days ± SE) and egg survival (% ± SE) of *T. absoluta* on Bravo and Tex 317 tomato lines at constant (25 °C) and alternating (30/20 °C) temperature regimes, photophase 12 h and RH 70 ± 10%. Means followed by same letter in columns do not significantly differ; Tukey test (P > 0.05).

Line	T °C	n	Egg development time (days)	Egg survival (%)
Bravo	30/20	100	3.90 ± 0.13 A	96 ± 2.66 A
Tex 317	30/20	100	4.08 ± 0.22 A	62 ± 9.04 B
Bravo	25	100	3.56 ± 0.08 A	98 ±2.00 A
Tex 317	25	100	3.92 ± 0.26 A	69 ± 8.35 B

Table 2. Width of cephalic capsule of *T. absoluta* larvae kept in leaflets of Bravo (30/20 °C), Bravo (25 °C), Tex 317 (30/20 °C) and Tex 317 (25°C) tomato lines, 12 h photophase and RH 70 ± 10%.

Instar	Cephalic capsule width (mm)		
	Variation interval	Mean	95% confidence interval
	Bravo 30/20 °C		
I	0.15	0.15	0.150 - 0.150
II	0.22 - 0.25	0.247	0.246 - 0.250
III	0.38 - 0.40	0.381	0.380 - 0.383
IV	0.50 - 0.63	0.571	0.567 - 0.575
	Bravo 25 °C		
I	0.15 - 0.20	0.152	0.151 - 0.154
II	0.25 - 0.27	0.254	0.254 - 0.256
III	0.38 - 0.45	0.392	0.390 - 0.395
IV	0.50 - 0.66	0.577	0.574 - 0.581
	Tex 317 30/20 °C		
I	0.15	0.15	0.150 - 0.150
II	0.25 - 0.27	0.25	0.250 - 0.252
III	0.38 - 0.43	0.395	0.394 - 0.397
IV	0.53 - 0.61	0.582	0.579 - 0.585
	Tex 317 25 °C		
I	0.15	0.15	0.150 - 0.150
II	0.22 - 0.27	0.242	0.240 - 0.244
III	0.35 - 0.43	0.386	0.385 - 0.388
IV	0.50 - 0.63	0.568	0.566 - 0.572

Fertility life table

To be able to estimate the population growth of *T. absoluta*, fertility life tables were determined for each treatment, through the survival rate (l_x) and specific fertility (m_x). The fertility life table parameters recorded were: net reproductive rate (R_0) (number of females/female); the intrinsic rate of increase (r_m) (a parameter related to the speed of population growth); mean generation time (T) (the average period between the birth of individuals of one generation and the next); the finite rate of increase (λ) (the multiplication factor of the original population per unit of time); and time required for the population to double in number (TD). For a detailed explanation of these parameters and the way how they are calculated, see Maia *et al*. (2000).

Data analysis

The data from egg, larval, pupal and egg to adult development were submitted to one-way analysis of variance and when significant differences among the averages were found, they were compared with the Tukey test at 5%, using the statistical software R Development Core Team (2009). To determine the number of instars, a multimodal curve was drawn with the overlap of the confidence intervals ($P < 0.05$) from the cephalic capsule widths among the successive instars (Giustolin *et al*., 2002). The sex ratio was analyzed with the Kruskal-Wallis test at 5% (Theodorsson-Norheim, 1986). The data on duration of pre-oviposition, oviposition, post-oviposition periods, number of eggs and adult longevity were submitted to one-way analysis of variance, and when significant differences were found between the means, these were compared by Tukey test at 5%. The means of life table parameters were estimated by the Jackknife technique (Maia *et al*., 2000).

Results

Development of egg, larva, pupa and egg to adult

Egg development time of *T. absoluta* did not show significant differences between temperature regimes and tomato lines. Egg development ranged from 3.6 ± 0.16 to 4.1 ± 0.24 days (F = 1.30; df = 3; P = 0.2903) (table 1).

Based on measurements of cephalic capsule widths, we can conclude that *T. absoluta* has four larval instars (figure 1). The width of the cephalic capsules increased with larval stage in all treatments and are similar for instars in the same stage at the different treatments (table 2).

Development time of the 1st instar was significantly longer (3.20 days) (F = 9.32; df = 3; P = 0.0001) at 30/20 °C on the two tomato lines than at 25 °C constant (2.0 days on Bravo and 2.4 days on Tex 317). Development of the 3rd instar was significantly shorter on Bravo at 25 °C than for the other three treatments (F = 8.72;

df = 3.14; P = 0.0001). Development of 2nd and 4th instars did not show any significant difference for all treatments (table 3). Total larval development on Bravo was significantly shorter (F = 7.93; df = 3 P = 0.0001) (8.91 days) than on Tex 317 at 30/20 °C (10 days).

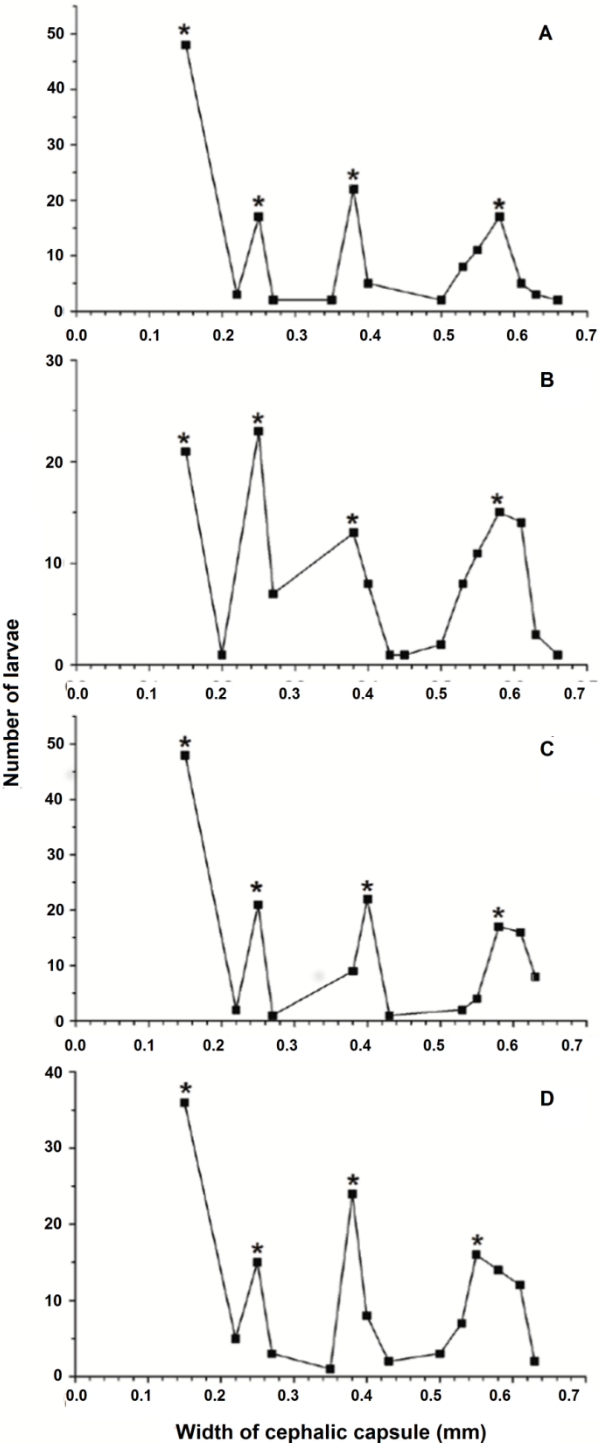

Figure 1. Multimodal distribution curve of the cephalic capsule width of *T. absoluta* larvae developing in leaflets of tomato lines (A) Bravo (30/20°C), (B) Bravo (25°C), (C) Tex 317 (30/20°C), (D) Tex 317 (25°C); 12 h photophase and 70 ± 10% RH. The asterisk above the line indicates four frequency peaks, related with number of instars.

Male pupal development on Tex 317 was significantly affected by temperature (F = 5.81; df = 3; P = 0.0039), and shorter (6.14 days) at 25 °C constant than at 30/20 °C (7.57 days) (table 4). Male pupae on Bravo at 30/20 °C showed a significantly longer development time (7.85 days) than male pupae on Tex 317 (6.14 days) at 25 °C. Temperature regime significantly influenced development time of female pupae as well (F = 6.40; df = 2.48; P = 0.0024) and in a similar way as it influenced male development (table 4).

Egg to adult development time was significantly influenced by tomato line and temperature regime. At 25 °C, the egg to adult development was significantly shorter (19.06 ± 0.56 days on Bravo and 20.52 ± 0.30 days on Tex 317) than at 30/20 °C on both tomato lines (21.8 ± 0.36 days on Bravo and 21.7 ± 1.19 on Tex 317) (F = 4.89; df = 3; P = 0.0048). At 25 °C constant, egg to adult development was shorter on Bravo than on Tex 317 (F = 7.52; df = 3; P = 0.0005), but no difference in development was found at 30/20 °C.

Juvenile survival, pupal weight and adult sex ratio

Egg survival of *T. absoluta* was significantly lower (F = 8.34; df = 3; P = 0.0002) on Tex 317 both at 25 °C (69%) and 30/20 °C (62%) than on Bravo (≥ 96%) (table 1). Larval survival was significantly lower (F = 8.32; df = 3; P = 0.0002) when they developed on Bravo at 30/20 °C and on Tex 317 at 30/20 °C and 25 °C, with survival rates of 72%, 61% and 70%, respectively, than on Bravo at 25 °C constant where survival was 98.20%. The survival rate of *T. absoluta* pupae was 100% for all treatments.

Pupal weights for males and females did not significantly differ when reared on different tomato lines or at constant or alternating temperature, with one exception: female pupae of Tex 317 developing at 25 °C were significantly heavier than males reared on the same line in the same conditions (F = 0.76; df = 3; P = 0.039).

The sex ratio of *T. absoluta* was significantly influenced by the temperature (H = 8.59; df = 3.16; P = 0.0001). Independent from the tomato line on which they were reared, the number of females was significantly higher at the alternating temperatures (30/20 °C) than at constant temperatures (25 °C). At alternating temperatures, the sex ratio (expressed as fraction females) was 0.5 on Bravo and 0.6 on Tex 317; at constant temperature, the sex ratio was 0.4 on Bravo and 0.3 on Tex 317.

Pre-oviposition, oviposition and post-oviposition periods, and fecundity

Pre-oviposition periods of *T. absoluta* did not significantly differ when reared on different tomato lines or at constant or alternating temperature and ranged from 0.47 to 1.13 days. However, the oviposition period was significantly shorter (10.87 days) (F = 8.42; df = 3.18; P = 0.0001) on Bravo at 25 °C constant than in the other treatments. On Bravo at 30/20 °C and on Tex 317 at 25 °C and 30/20 °C, *T. absoluta* kept ovipositing for at least 3.5 days more (14.33, 16 and 15.47 days, respectively) (table 5) compared to females kept on Bravo at 25 °C. The total number of eggs per female of *T. abso-*

Table 3. Development time of larval instars (I-IV) and total larval development (TT) (days ± SE) and larval survival (% ± SE) of *T. absoluta* kept on Bravo and Tex 317 tomato lines at 25 and 30/20 °C, 12 h photophase and RH 70 ± 10%. Means followed by same letter in columns do not significantly differ, Tukey test (P > 0.05).

Line	T °C	I	II	III	IV	TT	Survival
Bravo	30/20	3.20 ± 0.14 A (n= 48)	1.47 ± 0.13 A (n= 22)	1.93 ± 0.07 A (n= 29)	3.27 ± 0.23 A (n= 49)	9.87 ± 0.29 AB (n= 148)	72.00 ± 5.14 B (n=100)
Tex 317	30/20	3.20 ± 0.14 A (n= 48)	1.47 ± 0.13 A (n= 22)	2.13 ± 0.13 A (n= 32)	3.20 ± 0.22 A (n= 47)	10.00 ± 0.32 A (n= 149)	61.00 ± 9.92 B (n= 100)
Bravo	25	2.00 ± 0.19 B (n= 31)	1.82 ± 0.12 A (n= 26)	1.27 ± 0.14 B (n= 22)	3.82 ± 0.12 A (n= 49)	8.91 ± 0.09 B (n= 128)	98.20 ± 1.20 A (n= 100)
Tex 317	25	2.40 ± 0.16 B (n= 36)	1.53 ± 0.13 A (n= 18)	2.33 ± 0.13 A (n= 33)	3.60 ± 0.19 A (n= 54)	9.87 ± 0.29 AB (n= 141)	70.00 ± 2.73 B (n= 100)

Table 4. Weight (mg), and development (days) of pupae of *T. absoluta* reared on Tex 317 and Bravo tomato lines at temperatures of 25 and 30/20 °C, photophase of 12 h and RH 70 ± 10%. Means followed by the same capital letters in columns and lowercase letters in lines do not significantly differ, Tukey test (P > 0.05).

Line	T °C	Weight (mg)		Development time (days)	
		Male (n = 10)	Female (n = 10)	Male (n = 10)	Female (n = 10)
Bravo	30/20	3.11 ± 0.11 Aa	4.14 ± 0.22 Aa	7.85 ± 0.34 A	7.57 ± 0.29 A
Tex 317	30/20	2.94 ± 0.19 Aa	4.04 ± 0.14 Aa	7.57 ± 0.36 A	7.14 ± 0.26 AB
Bravo	25	2.8 ± 0.20 Aa	3.91 ± 0.11 Aa	7.14 ± 0.26 AB	6.57 ± 0.20 BC
Tex 317	25	2.8 ± 0.20 Ab	4.28 ± 0.15 Aa	6.14 ± 0.26 B	6.00 ± 0.30 C

Table 5. Pre-oviposition, oviposition and post-oviposition periods of *T. absoluta,* total number of eggs per female and longevity of male and female developed on two tomato lines under constant and alternating temperatures of 25 and 30/20 °C, 12 h photophase and 70 ± 10% RH. Means followed by the same capital letters in columns and lowercase letters in lines do not significantly differ. Tukey test (P > 0.05).

Line	T °C	Couples (n)	Pre-ovip. (days)	Oviposition (days)	Post-ovip. (days)	Total eggs/female	Longevity (days)	
							Female	Male
Bravo	30/20	15	1.13 ± 0.13 A	14.33 ± 0.84 A	2.00 ± 0.68 B	172.47 ± 8.45 A	17.47 ± 0.89 Ba	19.6 ± 0.88 Aba
Tex 317	30/20	15	1.00 ± 0.14 A	15.47 ± 0.79 A	6.20 ± 0.72 A	153.93 ± 16.74 A	22.67 ± 0.83 Aa	23.00 ± 0.8 Aa
Bravo	25	15	1.07 ± 0.32 A	10.87 ± 0.59 B	3.60 ± 0.73 AB	172.73 ± 17.29 A	15.53 ± 0.60 Ba	16.47 ± 0.77 Ba
Tex 317	25	15	0.47 ± 0.22 A	16.00 ± 0.93 A	5.07 ± 0.94 A	200.73 ± 13.27 A	21.53 ± 1.24 Aa	21.07 ± 1.21 Aa

luta was not significantly different between the treatments and ranged from 153.93 to 200.73 eggs (table 5). Regardless of the tomato line and temperature regime, females laid at least 60% of their eggs during the first four days of the oviposition period (figure 2), and peaked for all treatments on the second day.

Temperature and tomato line significantly influenced the post-oviposition period of *T. absoluta* (F = 5.56; df = 3; P = 0.0021). Adults originating from larvae kept on Bravo showed a post-ovipositon period of two days at 30/20 °C, while individuals originating from larvae fed on Tex 317 showed a post-oviposition period of 5.07 days at 25 °C and 6.20 days at 30/20 °C (table 5).

Longevity

Tomato line and temperature regime significantly influenced longevity of males and females of *T. absoluta* (table 5). Females originating from larvae fed on Tex 317, independent from the temperature regime had a longer life span at both temperatures (22.67 days at 30/20 and 21.53 days at 25 °C) (F = 13.35; df = 3.42; P = 0.0001) than on Bravo (17.47 days at 30/20 and 15.53 days at 25 °C). The longevity of males was significantly different (F = 8.76; df = 3.42; P = 0.0001) on Bravo at 25 °C. Males originating from larvae fed on Tex 317 had a longer life span (average 21.53 days), than males originating from larvae kept on Bravo (average 15.53 days).

Population growth parameters

Tomato line and temperature regime significantly influenced age specific fertility (m_x) and survival rate (l_x) of females of *T. absoluta*. The survival curve (l_x) on both tomato lines and temperatures was of type I, showing high survival during the first 13-20 days of adult life, followed by a constant mortality rate after this first period of high survival (figure 3). Adults kept on Tex 317 at 30/20 °C started to die when they were 19 days old, while on Bravo the first adults started dying when they were 10 days old (figure 3). The highest fecundity (m_x) was observed during the 2nd day of females on Bravo and Tex 317 at 25 °C and at 30/20 °C, and ranged from 13 to 24 eggs (figure 3).

The net reproductive rate (R_0) of *T. absoluta* significantly differed between the two tomato lines. On Bravo the R_0 was 59.40 and 68.30, while on Tex 317 the R_0

was 29.10 and 40.10 at 30/20 °C and 25 °C, respectively (table 6). All values of the intrinsic rate of increase (r_m) were positive, showing population increase in all treatments. Nevertheless, the population growth of *T. absoluta* was significantly lower on Tex 317 at 30/20 °C (table 6) than in the other treatments. The finite rate of increase (λ), also was significantly lower on Tex 317 at 30/20 °C, than in the other treatments (table 6). The mean time between generations (T) was significantly lower on Tex 317 at 25 °C than in the other treatments. The time required for the population to double in number of individuals (TD) was significantly longer on Tex 317 at 30/20 °C than in the other treatments (table 6).

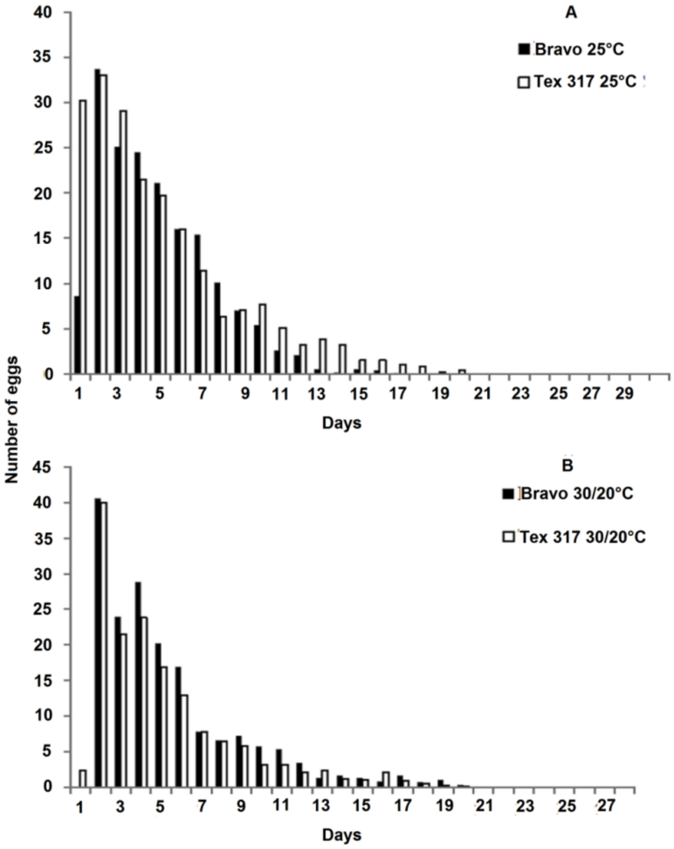

Figure 2. Daily oviposition of *T. absoluta* on Bravo and Tex 317 tomato lines at constant (A) (25 ºC) and alternating (B) (30/20 °C) temperature regimes, photophase 12 h and RH 70±10%.

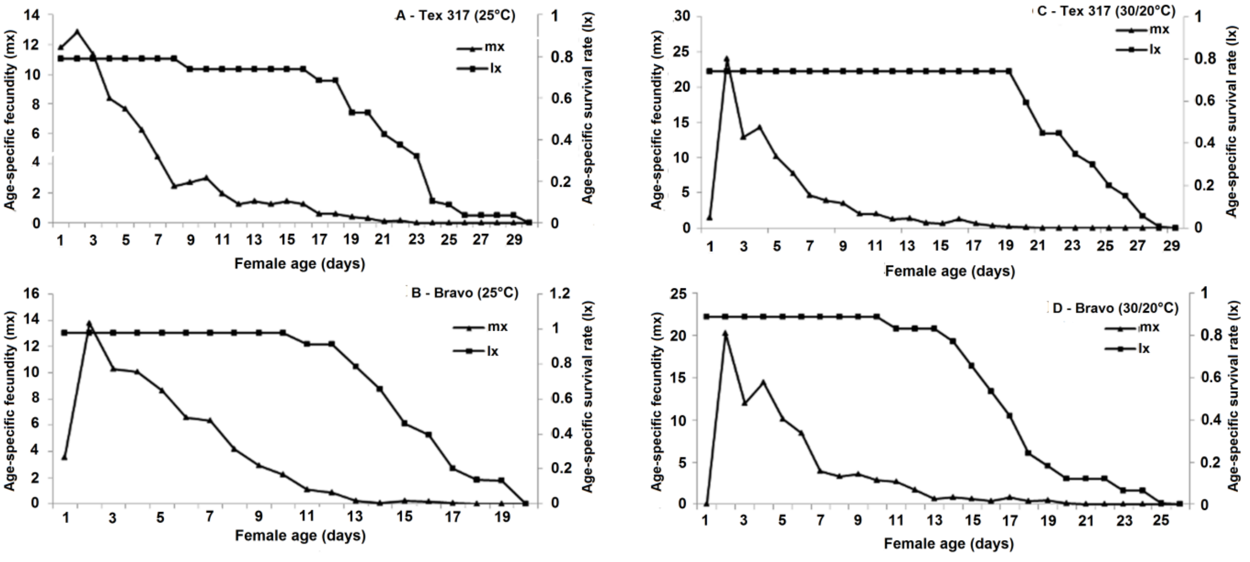

Figure 3. Age-specific fecundity (m_x) and age-specific survival rate (l_x) of *T. absoluta* on tomato lines (A) Tex 317 (25°C), (B) Bravo (25°C), (C) Tex 317 (30/20°C), (D) Bravo (30/20°C), photophase 12 h and RH 70 ± 10%.

Table 6. Fertility life table parameters of *T. absoluta,* developed on two tomato lines under constant and alternating temperatures of 25 and 30/20 °C, 12 h photophase and 70 ± 10% RH. Fifteen females were evaluated per tomato line and temperature regime. (R_0 = net reproductive rate; T = mean generation time; r_m = intrinsic rate of increase; TD = time required for the population to double in number; λ = the finite rate of increase).

Line	T °C	Growth parameters				
		R_0	T	r_m	TD	λ
Bravo	30/20	59.40 A	26.10 A	0.15 A	4.40 B	1.16 A
Tex 317	30/20	29.10 C	26.40 A	0.12 B	5.40 A	1.13 B
Bravo	25	68.30 A	26.30 A	0.16 A	4.30 B	1.17 A
Tex 317	25	40.10 B	24.60 B	0.15 A	4.60 B	1.16 A

Discussion

Development, survival, weight, sex ratio and reproduction

Temperature regime and tomato line influenced almost all parameters we determined for the immature stages of *T. absoluta*.

Egg development times of *T. absoluta* were, in general, similar to those reported by other authors (Fernández and Montagne, 1990; Imenes *et al*., 1990; Bogorni and Carvalho, 2006), but shorter than those found by Duarte *et al*. (2015). An interesting finding is that egg survival on lines Tex 317 is significantly lower at both temperature regimes than on Bravo, which might be the result of antibiosis resistance and an effect of toxic substances (Eigenbrode and Trumble, 1993; 1994). Egg survival of *T. absoluta* on tomato cultivars Santa Clara and Empire was on average 89.4% (Bogorni and Carvalho, 2006), and ranged between 75.7% and 95.0% on other tomato cultivars (Imenes *et al*., 1990; Giustolin and Vendramim, 1994; 1996).

Fast temperature changes and particularly exposure of insects to low temperatures result in a reduction of the metabolic rate and, consequently, in slower development (Roy *et al*., 2002). The first instar larvae in this study showed significantly longer development at the alternating temperature than at the constant temperature and was independent of the tomato line. Possibly, due to their small size, the first instar larvae are more susceptible to abrupt changes in temperature than instars II-IV for which we did not find differences in development. The average time for *T. absoluta* to reach the fourth instar at 25 °C constant was longer on Tex 317 than on Bravo. Bogorni and Carvalho (2006) found at 25 °C also a longer developmental time for 1st instars on tomato cultivar Carmen than on Bravo. Duarte *et al*. (2015) found longer development times for larvae and pupae in most cases on cultivar Vyta at the same temperature regimes we tested. Differences in development time of immature stages when reared on various cultivars indicate differences in host-plant resistance (Lara, 1991). At 30/20 °C the longest egg to adult development was found on Tex 317 compared to individuals exposed to both lines at 25 °C and on Bravo at 30/20 °C. An increase in immature developmental time can be attributed to changes in abiotic conditions, as well as to a low food conversion efficiency caused by suboptimal food or food with toxic substances in the food supplied, indicating the presence of antibiosis resistance (Baldin *et al*., 2007). The longer development of immature stages on Tex 317 line which we found in this study is interesting, as it will result in a lower number of pest generations and also the larvae will be exposed to natural enemy attack for a longer period (Brunherotto *et al*., 2010).

At 25 °C constant, *T. absoluta* showed lower larval survival on Tex 317 than on Bravo. Several other genotypes which showed resistance to *T. absoluta* had survival percentages similar to the survival we found on Tex 317 (Thomazini *et al*., 2001), though Duarte *et al*. (2015) found much lower larval survival values. The lower larval survival combined with longer larval development on Tex 317 supports the hypothesis that antibiosis is probably the mechanism involved in resistance to *T. absoluta* and this antibiosis resistance might be caused by chemical compounds (e.g. acyl sugar) in the leaves of tomato (Ecole *et al*., 2000; Maciel *et al*., 2011). Kennedy and Yamamoto (1979) considered the allelochemical 2-tridecanone in tomato leaflets as toxic to several species of insects, including *Helicoverpa zea* (Boddie), *Keiferia lycopersicella* (Walsingham), *Aphis gossypii* Glover and *Aphis craccivora* Koch. Resende *et al*. (2006; 2008) reported that a high content of acyl sugars in tomato leaves is the main factor causing resistance to pests. Genotypes with high acyl sugar content are currently selected in the search for resistant cultivars to *T. absoluta* (Maciel *et al*., 2011).

Male and female pupal weight was not influenced by the type of tomato line and temperature regime. Similar weight values were found by Thomazini *et al*. (2001) for pupae reared on tomato line Santa Clara at 25 °C. In our study, male pupae from Tex 317 showed similar weight to that observed in studies with cultivars that contain 2-tridecanona (2-T), a compound which provides resistance to *T. absoluta* (Thomazini *et al*., 2001; Bogorni and Carvalho, 2006). Pupae on both tomato lines developed faster at 25 °C than at 30/20 °C. Discrepancies are common between developmental times predicted from constant development-temperature relationships and those measured under natural alternating or alternating temperatures around the same mean (Mironidis and Savopoulou-Soultani, 2008; Carrington *et al*., 2013). Also, it is known that insects may show slower development at alternating than at constant temperatures (Petavy *et al*., 2001).

We have no explanation for the higher sex ratios found on both tomato lines at the alternating temperature regime compared with the sex ratios at the constant temperature.

The pre-oviposition period of *T. absoluta* females was not influenced by tomato line and temperature regime. Similar pre-oviposition periods for *T. absoluta* on tomato were reported by Borgoni and Carvalho (2006). Imenes *et al.* (1990) observed an average of one day, ranging from a few hours to three days. In our study, the oviposition period was shorter on Bravo at 25 °C and similar to the value found by Moreira *et al.* (2009) (8.7 days) on the susceptible cultivar Santa Clara.

The daily number of eggs laid by *T. absoluta* was similar for both tomato lines and temperature regimes. Similar data were found by Thomazini *et al.* (2001) and Bogorni and Carvalho (2006). Also, the total number of eggs laid by *T. absoluta* did not differ on both tomato lines and temperature regimes. Duarte *et al.* (2015) found a much lower number of eggs per female on cultivar Vyta. According to Mordue and Blackwell (1993), the number of eggs laid by insect females on leaf surfaces may vary due to the repellent activity of volatile compounds, causing irritability in the females at the time of oviposition. In our study such a repellent action was not observed.

We found an oviposition peak during the first days of egg laying. Similar observations were made by Bogorni and Carvalho (2006) and Fernández and Montagne (1990) at 25 °C on susceptible tomato cultivars.

Population growth parameters

The population growth parameters obtained from cohorts reared on different tomato lines and at constant and alternating temperatures are useful for the evaluation of the biotic potential of *T. absoluta* (Sánchez *et al.*, 1997). The survival rate (l_x), which is the probability of newly emerged *T. absoluta* to be alive at age x is related to the fecundity (m_x). Mortality of *T. absoluta* kept on Tex 317 at 30/20 °C was observed after 19 days, while on Bravo the first adults already died after 9 days. Survival rate data on Tex 317 were similar to those reported by Vivian *et al.* (2002) who found an increase in the mortality of *T. absoluta* from the 20th day of life in conditions of greenhouse at 30 °C.

The survival curve patterns (l_x) we found can be characterized as type I (Begon *et al.*, 1996), showing that mortality of *T. absoluta* is concentrated in older individuals for both tomato lines at both temperature regimes.

Most of the life table parameters show that the trends in fertility were similar on Bravo at 30/20 °C and on Bravo and Tex 317 at 25 °C. The lowest value for the finite rate of increase (λ) which was observed on Tex 317 at 30/20 °C can be explained by the increased time needed for the population to double in numbers of individuals (TD). Also the lowest value of R_0 and r_m were found on Tex 317 at 30/20 °C. The significantly lower value of R_0 on Tex 317 at both temperature regimes when compared with the R_0 on Bravo may be the result of antibiosis resistance, since the number of eggs laid by females in the two tomato lines showed no significant differences. In addition, a alternating temperature regime also negatively and significantly influenced population growth of *T. absoluta* on Tex 317, which corroborates the results of Garcia *et al.* (2006). Duarte *et al.* (2015) also found that a alternating temperature of 30/20 °C negatively influenced most population parameters and their data show that population growth on cultivar Vyta is much lower than on Bravo and Tex 317 that we tested.

The parameter r_m is an indicator for the growth potential of a population under specific environmental conditions (Jervis, 2005). On Tex 317 at 30/20 °C r_m is much lower than on the same line at 25 °C, than on Bravo at both temperature regimes. This provides a possibility for use of host-plant resistance in combination with biological control, if temperature fluctuations are as large in the field as we used in the laboratory. Allegedly, a natural enemy can effectively reduce a pest if, among other criteria, the intrinsic rate population growth of a parasitoid or the kill rate of a predator is equal to or greater than the intrinsic rate of population growth of the pest (van Lenteren, 2009). The parasitoid *Trichogramma pretiosum* Riley is a natural enemy of *T. absoluta* and has an r_m of 0.15 at 29/16 °C (Pratissoli *et al.*, 2007). As the value of the r_m of this natural enemy is superior to that of *T. absoluta* on Tex 317 at 30/20 °C ($r_m = 0.13$), the use of this parasitoid in combination with tomato line Tex 317 may open possibilities for biological control of the pest. Currently, we are evaluating a number of mirid predators (Bueno *et al.*, 2013) which have sufficiently high predation rates, i.e. similar to or higher than mirids which are successfully used for control of this pest in Europe (Urbaneja *et al.*, 2012), to consider them as serious candidates for control of *T. absoluta*.

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