




Seasonal variation in natural mortality factors of *Tuta absoluta* (Lepidoptera: Gelechiidae) in open-field tomato cultivation

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Abstract

The seasonal variation in natural mortality of phytophagous insects is determined by the relative importance of biotic and abiotic factors in agroecosystems. Knowledge regarding these factors throughout the year represents a key concern for IPM programmes. Seasonal population fluctuations of tomato pinworm, *Tuta absoluta*, led to an investigation of its natural mortality factors during the rainy season when the population level is low and during the dry season when population peaks occur. The aim of this study was to verify the seasonal variation in *T. absoluta* mortality factors in tomato crops. Immature stages of *T. absoluta* were obtained from laboratory-rearing in the laboratory. These were taken to the field and monitored over two years. The mortality causes for each stage of insect development from egg to adult were assessed daily. Multiple biotic and abiotic mortality factors affected the immature *T. absoluta* stages such as rainfall, physiological disturbances, diseases, parasitoids and predators. The key *T. absoluta* mortality factor during summer–spring was predation. In addition, larvae predation correlated positively with temperature, wind velocity, photoperiod and rainfall. Nevertheless, during winter–fall, the key mortality factor was parasitism. Therefore, the critical stage for mortality was 3rd- and 4th-instar larvae, being more vulnerable to natural control factors. Finally, the results showed the importance of vertical and horizontal action on natural mortality factors.

KEYWORDS

climatic elements, insect seasonality, parasitoid, physiological disturbance, predator, Tomato borer

1 | INTRODUCTION

Understanding how agroecosystem components can change the attack intensity of a pest species on its host plant is a key step in the development of integrated pest management (IPM) programmes (Pereira, Picanço, Bacci, Crespo, & Guedes, 2007; Semeão et al., 2012). This may be even more important when considering a crop system such as tomatoes, where pest insect control interventions are intensively carried out with synthetic insecticide applications. However, in some cases, the desired outcome was not achieved

due to control failures and pest resistance to insecticides (Campos, Silva, Silva, Silva, & Siqueira, 2015; Campos et al., 2014; Gontijo et al., 2013; Roditakis et al., 2015; Silva, Assis, Ribeiro, & Siqueira, 2016; Silva et al., 2011, 2015; Siqueira, Guedes, & Picanço, 2000). Therefore, the management practices adopted aim at conserving and increasing the role natural control agents play as agroecosystem components, being able to help to reduce losses due to pest attack. Such practices are environmentally safer and more sustainable since they have low or no negative economic impact on crop production.

Maintenance of pest population balance can be achieved through the action of several natural mortality factors (Pereira et al., 2007; Semeão et al., 2012). This kind of information can be obtained using ecological life tables from pest studies to determine the critical stage and key mortality factors of a pest (Gonring, Picanço, Guedes, & Silva, 2003; Pereira et al., 2007; Rosado et al., 2014; Semeão et al., 2012; Silva et al., 2017). Interaction relevance of leafminer in demographic parameters is affected between miners and host plants, such as miners' insects and natural enemies (vertical sources) or in intra- and inter-specific competition, including meteorological factors, such as wind, storms, frosts, heavy rain, moisture and extreme temperatures (horizontal sources; Auerbach, Connor, & Mopper, 1995). Seasonal variation in agroecosystems, such as rainfall and dramatic maximum/minimum temperature changes, can be the most important factors to reduce insect abundance (Cornell & Hawkins, 1995). Among the factors involved in natural mortality, natural enemies and climatic variables stand out because they cause mortality during all life cycle stages of insect pests and generally have a great impact on the population dynamics of these organisms (Naranjo & Ellsworth, 2005). These two groups of mortality factors may present seasonality throughout the crop cycle and during the different seasons (Pereira et al., 2007; Semeão et al., 2012). Therefore, it is important to know the duration and magnitude of these factors at different times, because this information is fundamental for population dynamics studies and sustainable development of pest management programmes.

The tomato pinworm, *Tuta absoluta* (Meyrick; Lepidoptera: Gelechiidae), is the main tomato pest in South America (Gontijo et al., 2013; Silva et al., 2011). Currently, this pest has been recognized as a worldwide threat to tomato production, being one of the major concerns as a quarantine pest for North American and Asian countries, where the presence of this pest has not yet been confirmed (Biondi, Guedes, Wan, & Desneux, 2018; Campos, Biondi, Adiga, Guedes, & Desneux, 2017; Desneux, Luna, Guillemaud, & Urbaneja, 2011; Desneux et al., 2010). This is a result of the high capacity of *T. absoluta* to cause economic damage to tomato crops due to its larvae attacking various parts of the plant such as the leaves, flowers, stems and especially fruits (Biondi et al., 2018; Galdino et al., 2015; Tropea Garzia, Siscaro, Biondi, & Zappalà, 2012). The losses caused by *T. absoluta* to tomato crops, depending on the time of year, may reach 100% (Desneux et al., 2011; Guedes & Picanço, 2012). This variability in attack is probably due to the seasonality of its population density. Considering that the harmfulness of *T. absoluta* depends on its abundance, understanding the mechanisms that determine its population regulation is fundamental in the elaboration of integrated pest management programmes.

Natural enemies and climatic conditions can overcome deficiencies in the method normally used to control *T. absoluta*, that is, synthetic insecticide applications, which are a critical IPM component that can greatly impact population dynamics of pests. Therefore, the objectives of this study were (a) to investigate the

impact of natural mortality factors on *T. absoluta*; (b) the seasonality of these mortality factors throughout the year in tomato crops; (c) and to determine the relationship between these components of *T. absoluta* mortality.

2 | MATERIALS AND METHODS

The study carried out in an experimental tomato crop area in Viçosa, Minas Gerais, Brazil (20°48'45"S, 42°56'15"W, altitude 600 m). The experimental setup was 12 rows with 30 tomato plants cv Santa Clara seedling in a spacing of 0.5 m between plants and 1 m between rows in a total area of 180 m². The experimental area used standard agronomic practices for tomato cultivation; however, no other method to control insects and diseases was used.

Seasonal and natural variabilities in *T. absoluta* mortality factors were evaluated using ecological life tables for eight different periods over two years. The assessments were performed for four seasons. The periods in each year were chosen to represent different seasons (fall, winter, spring and summer) for the Southern Hemisphere.

2.1 | Rearing of *Tuta absoluta*

The leaves of tomato plants with *T. absoluta* were collected from commercial crops and taken to the laboratory for study (Silva et al., 2011). A *T. absoluta* colony was established in the laboratory using a system of four wood cages (40 × 40 × 40 cm), covered with nylon mesh. The laboratory-rearing system consisted of cages for oviposition, 1st- and 2nd-instar larvae, 3rd- and 4th-instar larvae, pupae and adults. The *T. absoluta* colony in the laboratory was placed under conditions of 25 ± 2°C, relative humidity (RH) 75 ± 5% and photoperiod of 12:12 (L: D) hr. Larvae were fed with cv. Santa Clara tomato leaves from the greenhouse without insecticide application.

2.2 | Mating establishment

Tuta absoluta stages from laboratory-rearing were taken to field and their mortality monitored throughout the seasons. Ten experimental plots were used for each instar, with each plot having a tomato plant at the reproductive stage chosen at random from the crop. Egg and 1st-instar mortality was evaluated on the apical canopy. Second-, third- and fourth-instar *T. absoluta* mortality was evaluated on the median canopy. These canopy positions were selected for evaluation of mortality, because they are the preferred plant sites for female oviposition (Torres, Faria, Evangelista, & Pratisoli, 2001). Therefore, ten leaves from the apical canopy (plots with eggs and 1st-instar larvae) and ten from the median canopy with 2nd-, 3rd- and 4th-instar larvae were carefully inspected to the presence of *T. absoluta* eggs, larvae and pupae using 10× magnifier lens. If any egg, larva or pupa were found, they were removed with the aid of a soft paint brush

as well as any dust or eggs and larvae of other species that were present on the leaves.

During initial mating establishment, adult couples were kept in the laboratory. After mating, they were taken to field to obtain eggs. Thirty *T. absoluta* adults were placed in each plot, closed using nylon mesh, and were left for 24 hours for female oviposition. Eggs were counted using a 10× magnifying manual lens, and their positions on the tomato leaf were recorded using schematic drawing. In each plot, were left 150 eggs, totalling 1,500 eggs per season.

Two hundred and fifty larvae from each instar from the *T. absoluta* colony were used for larval stage establishment. From each instar, 25 larvae/plot were used. They were transferred using a fine-tipped brush. The different instars were identified through the degree of cuticle sclerotization, body size and larval cephalic capsule (Imenes, Fernandes, Campos, & Takematsu, 1990). At each larval stage, the insects were collected from the field at the beginning of the change to the next instar. An exception was made for the 4th-instar larvae, which were removed from the field when they presented a pinkish appearance, which is indicative of the change from larval stage to pupae (Imenes et al., 1990). This removal of insects occurred only at the end of the larval 4th instar, before pupal stage, and then, the larvae remained exposure during all the 4th-instar larval stage. This procedure was adopted, because the 4th-instar larvae generally migrate to the soil before they start to pupate.

A total the 300 individuals were selected from the field and grouped into 30 individual/plot to evaluate pupae mortality. The pupae were placed into plastic trays (5 × 25 × 30 cm) with a 1 cm layer of sand, which were placed underneath the tomato leaves in the pupation cages stored in the laboratory for 24 hr. After this period, the sand was sifted, and the pupae removed for use in the field. This was done due to *T. absoluta* pupae often being found in the soil or in the dry leaflets or stems of tomato plants (Imenes et al., 1990). The pupae from each plot were conditioned in plastic pots (10 cm in diameter and 7 cm of height), perforated on the side and at the base to allow water drainage from the occasional rains that occurred during the experimental period. The pupae were placed inside plastic pots with a thin layer of sand at the bottom of approximately 3 mm height. Then, the pots were placed at soil level next to the base of the tomato plant. In order to standardize the time of pupae removal from field, a pilot test was performed in the laboratory to measure the time taken for adult emergence.

2.3 | Assessment of mortality factors

Tuta absoluta mortality factors were monitored in the field from the beginning of the egg stage to the end of the pupal stage (Pereira et al., 2007; Semeão et al., 2012). Egg stage data were recorded, that is, position, dates and disappearance cause. The rainfall action on mortality of eggs was determined by counting the number of eggs before and after each rainfall event. It was considered a predator attack when eggs were not found in their previously registered positions and there had been no rain between two consecutive assessments. This assumption is plausible since the *T. absoluta* eggs remain

strongly adhered to the leaves making it difficult for the wind to dislodge them. Damaged eggs, which only presented chorion, were considered dead due to predation. The presence of predators on each leaf was recorded, and representative specimens were collected and placed in 70% ethanol for subsequent identification. The eggs which did not hatch were placed in the glass tube (10 cm length and 2 cm of diameter). The tubes were covered with perforated PVC plastic and stored in the laboratory under conditions of temperature at $25 \pm 0.5^\circ\text{C}$, RH $75 \pm 5\%$ and photoperiod 12:12 (L: D) hr for subsequent assessment of parasitoid emergence. Incubated eggs that did not present parasitoid emergence were considered dead due to inviability.

First-instar larvae mortality was evaluated in two stages: before and after they penetrated the leaves. The time for leaf penetration was 20–45 min (Imenes et al., 1990). Before leaf penetration, 1st-instar larvae that disappeared following rainfall were considered dead due to this factor, whereas in the absence of rainfall, they were considered dead due to predation. After leaf penetration (formation of the mines), larvae that disappeared or mines that were torn were considered dead due to predation. At the end of the 1st-instar stage, all the leaves evaluated at this stage were collected and analysed on a stereoscopic microscope (40× magnification). First-instar larvae that did not show signs of incomplete moulting (adhered to their exuvie) and disease symptoms were considered dead due to unknown factors (Pereira et al., 2007).

Second-, third-, and fourth-instar *T. absoluta* larvae that were found during mortality assessment dehydrated inside the mines, with ectoparasitoid, ecdysis disturbance or with disease symptoms were considered dead due to predatory bugs. However, *T. absoluta* larvae with disease symptoms had a mortality factor classified according to the symptoms caused by fungi or bacteria (Gouli, Gouli, & Marcelino, 2011). Larval mortality due to predation by predatory wasps was determined by the direct observation of this action on the *T. absoluta* mines which when attacked showed torn or removed surfaces. The mortality caused by other predators was determined by the observation of the direct action of their organisms on the larvae in the field. The same was the case with ectoparasitism, through evidence of larval paralysis and the observation of ectoparasitoids on *T. absoluta* larvae. Additionally, all the natural enemies found on the leaves were collected and their representative specimens were kept in 70% ethanol for complete identification. Like the egg stage, the effect of rain on larvae was determined by checking leaves immediately before and after rainfall. The mortality from rainfall was identified in the field by verifying dead larvae in mines flooded with water after the occurrence of this factor or by observation of drowning dead larvae trapped between leaf epidermis as the water evaporated.

The mortality was only attributed to predation when predators were visually observed feeding on egg, larval and pupal stages. Moreover, a parallel experiment was also carried out on the same fields to monitor the activity of the predators and identify the most frequent preying on *T. absoluta* stages according with the methodology used by Asiimwe et al. (2007). During this time, 24-hr checks

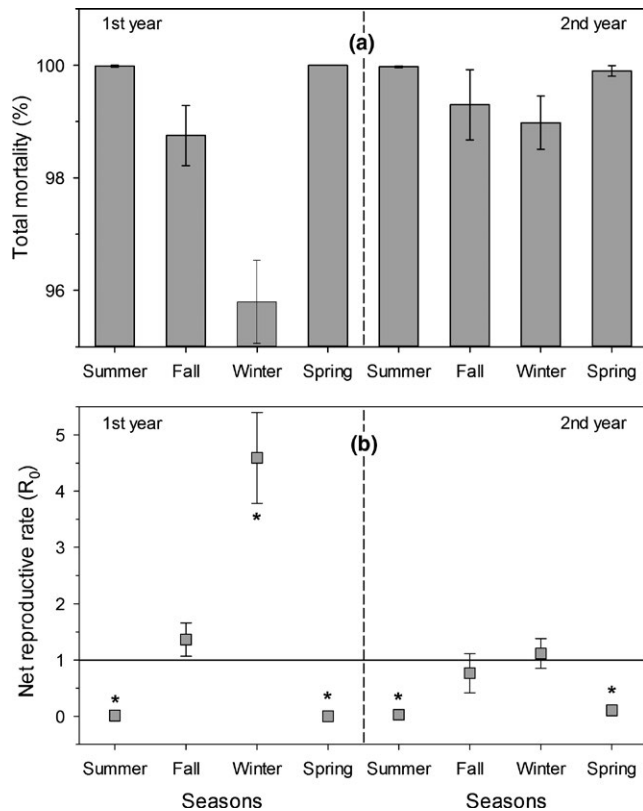


FIGURE 1 Seasonal analysis of *Tuta absoluta* life history of two parameters. (a) Differences in total mortality between seasons were compared using ANOVA and confidence interval at 95%. (b) Difference in net reproductive rate (R_0) between seasons. For each season, the R_0 was compared to an equilibrium value ($R_0 = 1$) using the t test. In Figure (a) are shown the mean values and 95% confidence intervals. In Figure (b) are shown the mean values and standard errors. Asterisks indicate that R_0 for those seasons is different from the equilibrium value

done at 3-hr intervals over a 1-month period at all the evaluated seasons were carried out.

To determine the level of parasitism, the 1st-, 2nd-, 3rd- and 4th-instar larvae alive at the end of each stage were transferred to new tomato leaves and conditioned in 500-ml plastic pots. The plastic pots with a 2-cm² hole in the top were covered with nylon mesh to allow for ventilation. The larvae were kept in the laboratory until the adult stage to verify parasitoid emergence two times a week on the same assessment date. New tomato leaflets were added to feed larvae. Emerged parasitoids were counted and kept in 70% ethanol for subsequent identification. Emerged *T. absoluta* adults were counted and removed from the plastic pots. Tomato leaflets were kept in the plastic pots until the *T. absoluta* adults or parasitoids were no longer observed.

During the pupal stage, natural mortality was determined by directly counting the number of pupae remaining in each plastic pot at the end of the period in the field. The number of pupae dead from predation was determined by the difference between the total initial pupae and pupae remaining in the plastic pots. The mortality was only attributed to predation when predators were visually observed

feeding on pupal stage. Remaining pupae were placed in a glass tube similar to the procedure adopted with un-hatched eggs. The pupae were kept in the glass tube for 30 days until *T. absoluta* adult or parasitoid emergence. After this, the pupae still in the glass tubes were classified as dead due to physiological disturbances (malformation) or rain. Pupae mortality due to rainfall was estimated in the laboratory where the experiment simulating the addition of rainfall to the plastic pupae pots under field conditions was realized. The daily rainfall volumes that occurred during the period that pupae remained in the field were recorded using a gauge installed in the crop. Rainfall action was attributed through the difference of pupae mortality between plastic pots that had added water and those that did not. Pupae that did not emerge *T. absoluta* adults were classified as dead due to physiological disturbances.

Tuta absoluta parasitoids were identified by Dra. Angélica Maria Penteado Martins Dias of the Universidade Federal de São Carlos, by Dr. Paulo Sérgio Fiuza Ferreira of the Universidade Federal de Viçosa and the Coleoptera by Dr. Ayr de Moura Bello. Others natural enemy specimens were collected, assembled and identified at the Entomology Museum of the Universidade Federal de Viçosa.

2.4 | Statistical analysis

For the parameters analysed, standard methods for building and ecological analysis of life tables were used (Southwood & Henderson, 2000). Significant differences in total mortality caused by natural mortality factors throughout the four seasons and the years were analysed using two-way ANOVA (PROC ANOVA) in SAS v.9.2 Software (SAS Institute, 2009). If a significance was detected, post hoc analyses were conducted using confidence interval at 95% (PROC UNIVARIATE SAS Institute, 2009). Since mortality levels can affect population growth, net reproductive rate (R_0) in each season was estimated and compared to a reference net reproductive rate ($R_0 = 1$) using a t test (TTEST Procedure) in the SAS v.9.2. The net reproductive rate data were calculated predicting how the *T. absoluta* population would behave in the light of the seasonality of the mortality factors. The net reproductive rate was estimate by division of egg number expected in the next generation (number of surviving adults in the current mating \times sexual rate \times fecundity) by the initial number of eggs in the current mating. The sex ratio (i.e., number of female/number of female + number of male) was considered to be 0.5973 with fecundity of 183 eggs/female (Mihsfeldt & Parra, 1999). This information was used because it allows for standardization with respect to sex and fecundity rates for all populations in the different seasons of the year. In this way, it was possible to demonstrate the impact of mortality on population development, without being affected by the reproductive biology of the insect.

The K value was determined to identify the difference between the mortalities by stage and mortality factors within each stage. The K value was calculated using the formula [$K = \log(100qx)$], where 100qx is the apparent mortality rate (Southwood & Henderson, 2000). The significant difference between mortalities by stage and mortality factors within each stage was analysed using one-way

ANOVA (PROC ANOVA) and, if a significance was detected, post hoc analyses were conducted using confidence interval at 95% (PROC UNIVARIATE SAS Institute, 2009).

For the *T. absoluta* critical stage and key mortality factor, a simple linear regression analysis of the partial K values of each stage or each mortality factor as a function of the total K values ($K = \sum k$) for $p < 0.05$ was performed for each period. The critical stage or key mortality factor was considered the one with the regression curve showing a higher slope coefficient at $p < 0.05$ (Pereira et al., 2007; Semeão et al., 2012). The difference between slopes was verified by the confidence interval at 95% probability.

The seasonality of mortality factors potentially associated with *T. absoluta* environmental factors such as wind velocity, rainfall, air temperature and photoperiod were analysed using principal component analysis (PCA) and other natural control agents using the program Canoco 4.5 system (ter Braak & Smilauer, 2002). The biplot ordering gradient was generated using CanoDraw 3.0. The response gradient was represented by the vectors with the origin at the centre point of the two axes of the sorting diagram. The vector length

is proportional to the significance of the variable. Vectors with the same direction and sorting represent a variable with positive correlation, while vectors with the same direction opposite represent a negative correlation. Variables were not correlated when the angle between the vectors is 90° .

3 | RESULTS

There were significant differences in the total mortality caused by the natural factors, considering different seasons of years ($F_{3;72} = 30.20$, $p < 0.001$), between the years ($F_{1;72} = 16.74$, $p < 0.001$) and in the interaction between seasons and year ($F_{3;72} = 12.19$, $p < 0.001$).

High *T. absoluta* mortality rates were observed in the summer and spring and low mortality was observed in the winter and fall during two years as was observed by confidence interval at 95% (Figure 1a). The *T. absoluta* net reproductive rate (R_0) was significantly higher than 1 in the winter in the first year (t test = 4.4, $df = 36$, $p = 0.001$). The R_0 of *T. absoluta* was significantly < 1 in the summer

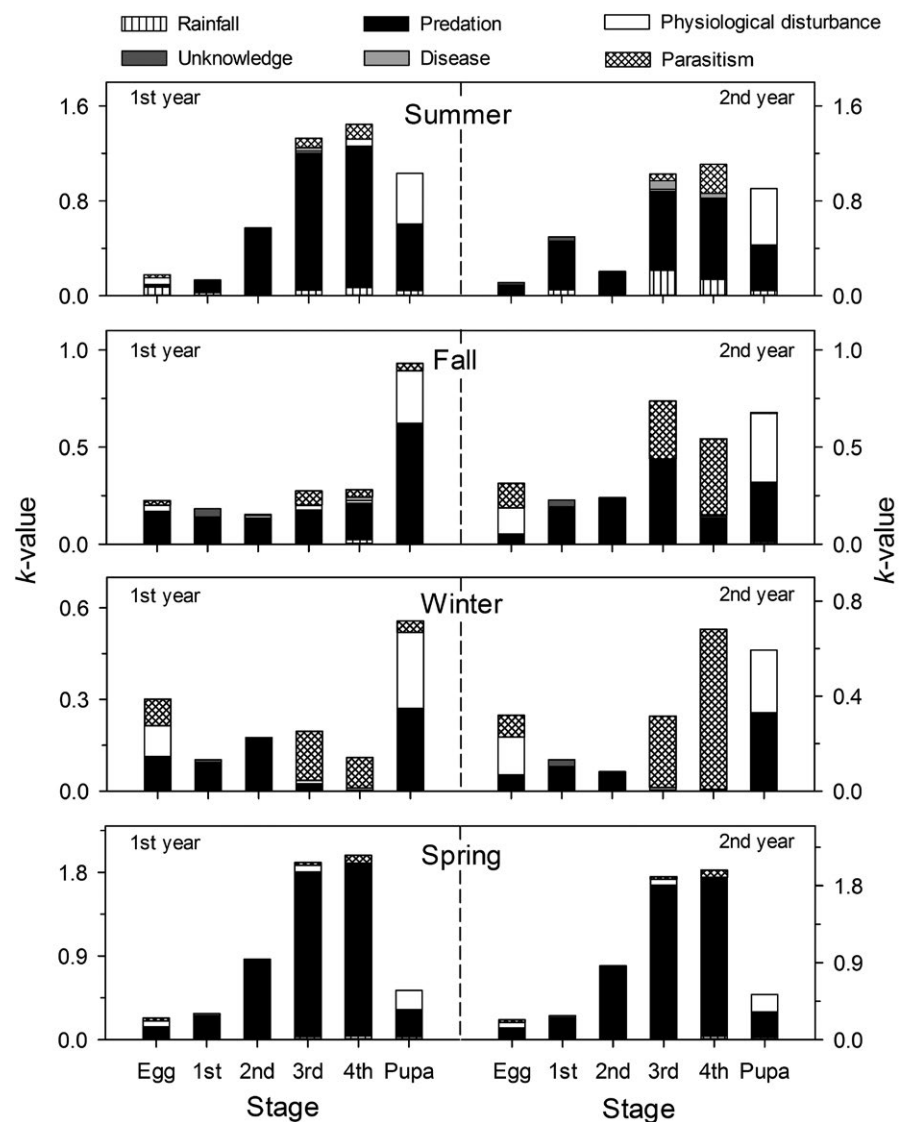


FIGURE 2 Relative proportion of mortality caused by different mortality factors and represented by K -value in each season. The x-axis represents the different stages and development stage of *Tuta absoluta*

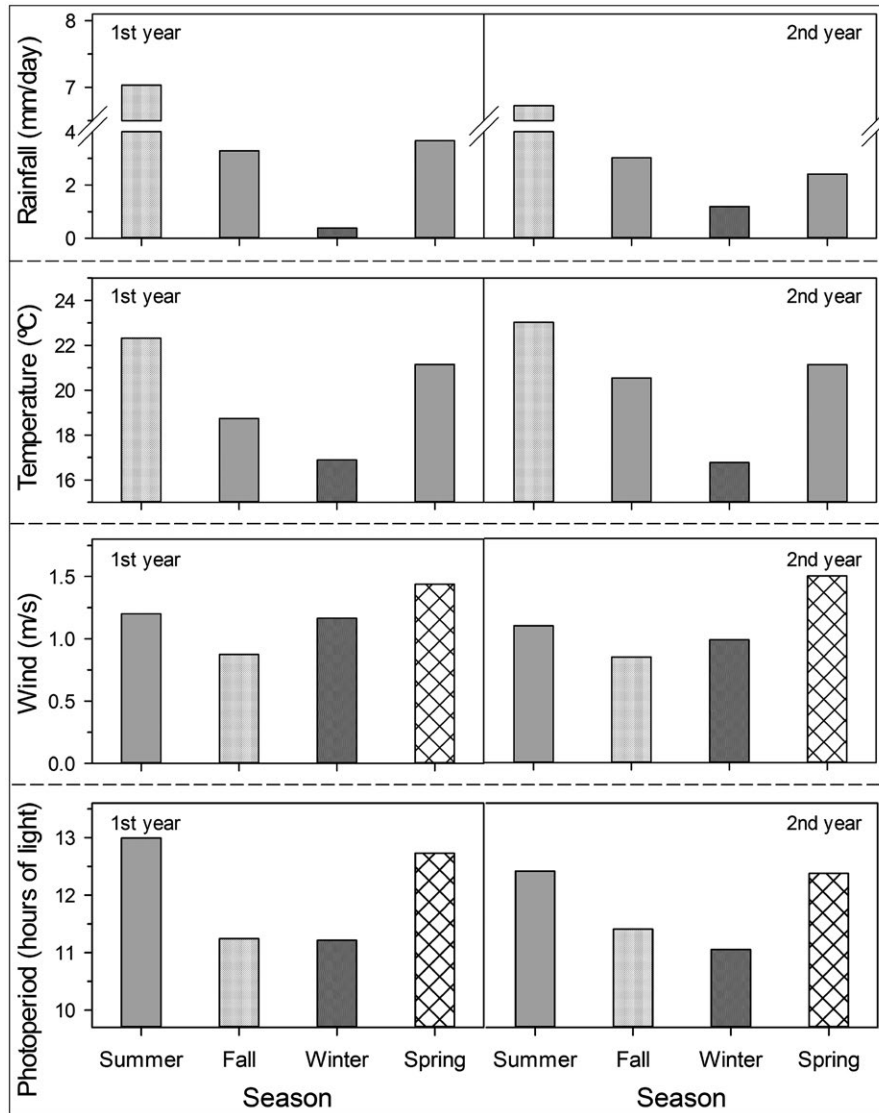


FIGURE 3 Seasonal variation in four environmental factors (rainfall, temperature, wind velocity and photoperiod) in four seasons. These factors were hypothesized affecting the *Tuta absoluta* survival in tomato crop

(t test = 102.1, $p < 0.001$) and spring (t test = 16.9, $df = 36$, $p < 0.001$) for 2 years. In the winter and fall, the R_0 was similar at 1 (Figure 1b).

Tuta absoluta mortality factors were rainfall, physiological disturbances, diseases, parasitoids and predators. The highest mortality factor for *T. absoluta* was predation (Figure 2). Predators caused mortality throughout all *T. absoluta* stages. Eighteen specimens were observed preying on *T. absoluta*. The predators from the eggs were from the thrip family: Phleothripidae, the pirate bugs *Blaptostethus pallescens* Poppius, *Orius tristicolor* White, and *Amphiareus constrictus* (Stål) (Heteroptera: Anthicoridae), and *Annona bimaculate* Distant and *Hyaliodocoris insignis* (Stål) (Heteroptera: Miridae), larvae of *Episyrphus* sp. (Diptera: Syrphidae), adults of *Acanthinus* sp. (Coleoptera: Anthicidae) and the ladybirds *Cycloneda sanguinea* (Linnaeus), *Psyllobora lenta* Mulsant, *Scymnus* sp. and *Hyperaspis* sp. (Coleoptera: Coccinellidae). The predators from larvae were the wasps *Brachygastra lecheguana* (Latreille), *Polybia scutellaris* (White) and *Protonecstarina sylveirae* (Saussure) (Hymenoptera: Vespidae).

The parasitoid caused mortality in all the *T. absoluta* stages. The *T. absoluta* egg parasitoid found was *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae). The larvae parasitoid found was *Bracon* sp. (Hymenoptera: Chalcididae) and *Pseudapanteles* sp. (Hymenoptera: Braconidae).

Less *T. absoluta* mortality due to predators occurred during winter in comparison with the other seasons ($F_{3;76} = 92.20$, $p < 0.001$). Rainfall caused 10 times more *T. absoluta* mortality during summer than in winter/fall and two times more than during spring ($F_{3;76} = 90.57$, $p < 0.001$). Physiological disturbance caused *T. absoluta* mortality during the fall and winter ($F_{3;76} = 3.92$, $p = 0.011$). *Tuta absoluta* mortality due to disease was high during the summer ($F_{3;76} = 3.05$, $p = 0.033$; Figure 2).

In summer, the quantity of rainfall was around 2–5 times higher compared with the other seasons. Temperature changes in subtropical regions are generally not drastic. However, they can cause mortality due to cold, although the temperature was colder during

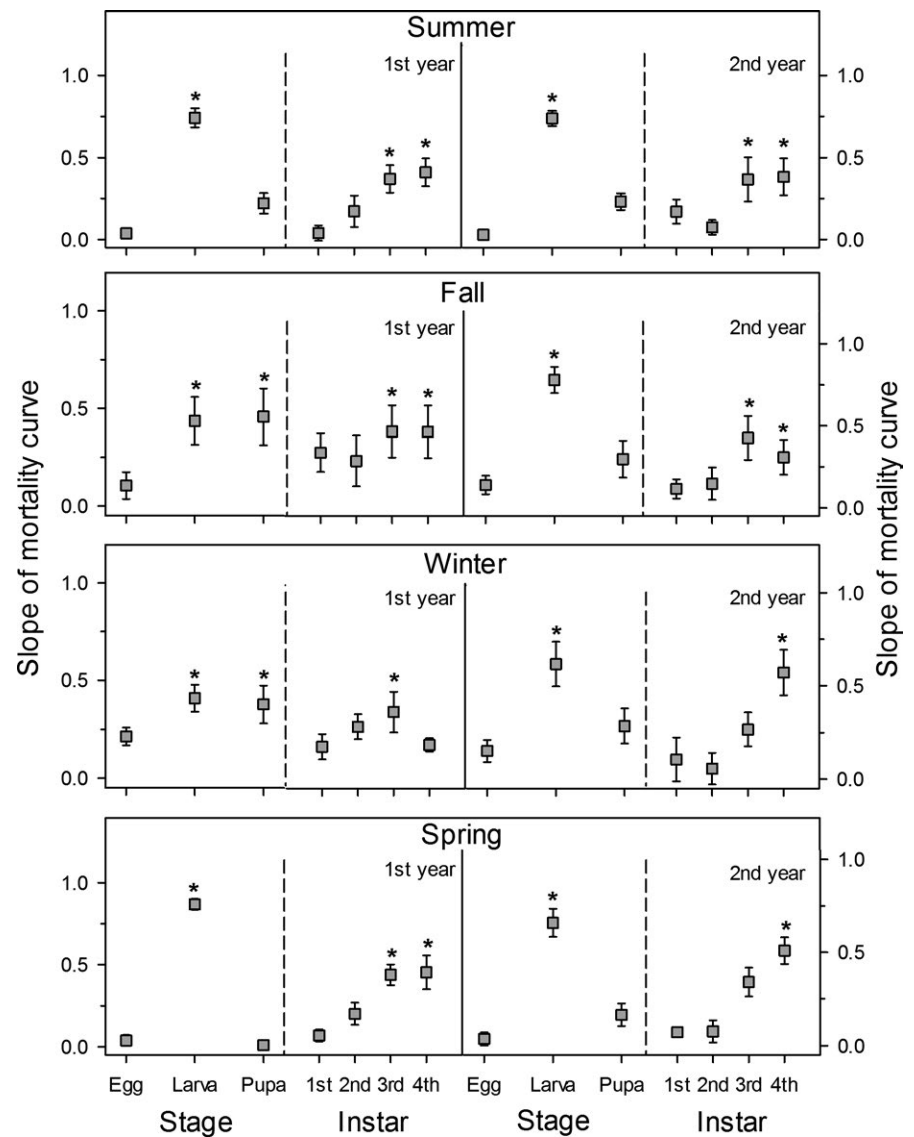


FIGURE 4 Critical stage (left side) and critical instar (right side) of *Tuta absoluta* mortality during four seasons. Regression linear analysis of partial K of each instar with a function of total K ($K = \sum k$) at $p < 0.05$ was performed at the critical stage with those with a regression curve showing the highest slope coefficient at $p < 0.05$. In Figure 4 are shown the slope coefficient of regression curve and confidence intervals of slope coefficient. Asterisks indicate difference in slope coefficient between stages or instar based in the confidence interval at 95%

winter, being a temperature that may reduce reproduction, it did not cause mortality (Figure 3). Variable wind velocity was observed (less intense during fall than during spring). Nevertheless, wind velocity could be a factor that caused *T. absoluta* mortality. The photoperiod was relatively similar between the different study periods (Figure 3).

Among *T. absoluta* stages, the larvae presented the mortality curve with the highest slope. However, this was not observed during fall or winter in the first year when both larvae and pupae presented a mortality curve with a high slope. However, they did not differ from each other. Among *T. absoluta* larval instar, the 3rd and 4th instar presented a mortality curve with the highest slope. On the other hand, during the winter, the mortality curve with the highest slope was observed in the 3rd instar. Additionally, during spring and winter in the second year, the mortality curve with the highest slope was for the 4th instar (Figure 4). Therefore, these were the critical stages for *T. absoluta* mortality for each year and season.

Generally, predators were the key *T. absoluta* mortality factor. Nevertheless, during the winter of the second year the key mortality factor was parasitism. The key factor of *T. absoluta* mortality during

winter in the first year and fall of the second year was physiological disturbances and larval parasitoids (Figure 5).

The PCA model for key *T. absoluta* mortality factors with the climatic elements generated four axes (Eigenvalue = 0.96) accounting for 99.4% of variance observed. During the larval stage, predation and parasitism were negatively correlated. During the pupal stage, predation and physiological disturbance were negatively correlated. Predation of 3rd- and 4th-instar *T. absoluta* larvae (the critical stage of mortality) correlated positively with total mortality and finally correlated negatively with the R_0 . The predation of larvae correlated positively with temperature, wind velocity, photoperiod and rainfall. The opposite was observed with the parasitism of *T. absoluta* larvae (Figure 6).

4 | DISCUSSION

Phytophagous insect populations respond idiosyncratically in time and space to a myriad of abiotic and biotic factors leading to seasonal

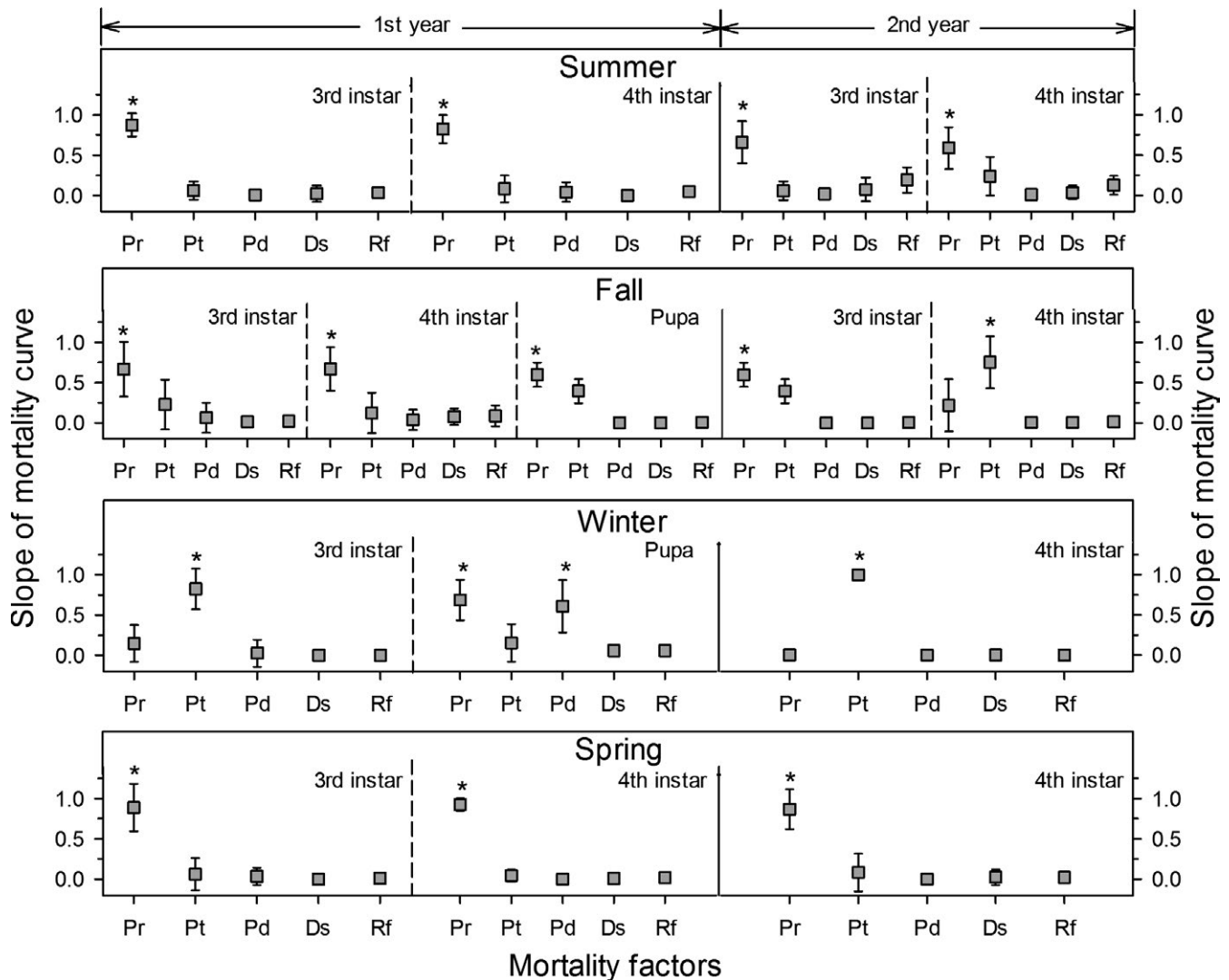


FIGURE 5 Key mortality factors of *Tuta absoluta* in summer, fall, winter and spring. Regression linear analysis of partial k of each mortality factor as a function of a total K ($K = \sum k$) at $p < 0.05$ was performed being the key factor mortality those with a regression curve showing the highest slope coefficient at $p < 0.05$. In Figure 5 are shown the slope coefficient of regression curve and confidence intervals of the slope coefficient. Asterisks indicate difference in slope coefficient between stages or instar based in the confidence interval at 95%. (Pr = predation, Pt = parasitism, Pd = physiological disturbance, Ds = disease and Rf = rainfall)

variation in population density (Campos, Schoederer, & DeSouza, 2006; Hopkins & Memmott, 2003; Yarnes & Boecklen, 2005). In this study, *T. absoluta* mortality varied seasonally and this variation was regulated by the relative importance of natural mortality factors for this pest that operate during each season of the year. The action of natural *T. absoluta* control factors caused higher mortality during summer and spring than in fall and winter. This variation in mortality may occur due to differences in precipitation during the summer and spring periods. The results obtained were in agreement with population fluctuation patterns for *T. absoluta* observed in the tropical region (Castelo Branco, 1992) and reinforce the importance of rainfall as a mortality factor for this pest. In addition to directly affecting mortality, rainfall can cause asynchrony in the emergence of adults and consequently delay mating and reduce female oviposition (Michereff, Vilela, Nery, & Thiebaut, 2004), therefore playing

an important role in population dynamics. Although rainfall was reported as the main factor responsible for the seasonality of phytophagous insects in the tropical regions, other factors such as predators, parasitoids, pathogens and physiological disturbances have a great influence on seasonal variation in *T. absoluta* populations as was verified in this study.

The *T. absoluta* population tended to increase during winter and decreased in summer as was observed with the net reproductive rate (R_0) for these periods. These results provided strong evidence for action of natural control factors to maintain *T. absoluta* populations at a balanced level. Therefore, it may reduce the need for insecticide applications, which are currently the method most used for *T. absoluta* control (Campos et al., 2014, 2015; Roditakis et al., 2015; Silva et al., 2015, 2016). However, a slight reduction in mortality during fall and winter led to an increase in R_0 , although the

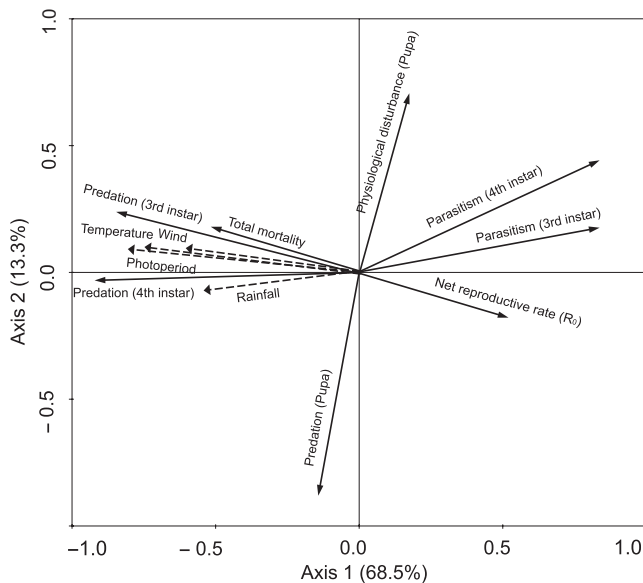


FIGURE 6 Ordination diagram of principal component analysis (PCA) of temperature effect of air ($^{\circ}\text{C}$), rainfall (mm/month), wind velocity (m/s) and photoperiod (hours of light/day) on the different mortality natural factors of *Tuta absoluta*. The contribution rates of the first 2 principal components were 68.50% and 13.30%, respectively. Variable with correlation has vectors with opposite direction and orientation. Perpendicular vectors indicate variables independent or no correlated

temperature during these periods was not optimal for *T. absoluta* reproduction or survival (Martins et al., 2016). Therefore, in IPM of *T. absoluta*, strategies that maximize the action of natural mortality factors should be included, especially during fall and winter, because a slight reduction in mortality in these seasons could increase the damage caused by *T. absoluta* in the following seasons.

Analyses of critical stages and key mortality factors were widely used in ecological life-table studies. The larval stage was the critical mortality stage for *T. absoluta* and similar results were previously reported in other ecological life-table studies for *T. absoluta* (Gonring et al., 2003; Pereira et al., 2007). In fact, the larval stage has a longer development period (20 days) than other stages such as egg (4 days) and pupae (7 days). Therefore, it could remain exposed for longer to natural mortality factors (Miranda, Picanço, Zanuncio, & Guedes, 1998). During the larval stage, the 3rd and 4th instars were the most vulnerable to mortality factors. Vulnerability during this stage could be related to the greater conspicuity of its larvae to natural enemies due to their body size (Cornell & Hawkins, 1995; Picanço et al., 2011). Another explanation for *T. absoluta* larvae vulnerability to rainfall action could be due to their sheltering in large mines, which were flooded after rainfall. Therefore, *T. absoluta* mortality during the final-larval instar reinforces the importance of maintaining an abundance and diversity of natural agents to control this pest.

Several predators such as predatory thrips, ladybugs *C. sanguinea*, *P. lenta*, *Scymnus* sp. and *Hyperaspis* sp., marmalade hoverfly *Episyrphus* sp., beetle *Acanthinus* sp., lacewing *Chrysoperla* sp. (Neuroptera, Chrysopidae) and small beetles *Paederus* sp. (Coleoptera: Staphylinidae) were found attacking *T. absoluta* on

tomato plants. The members of Phlaeothripidae, Coccinellidae, Anthicidae and Staphylinidae families have been previously cited as *T. absoluta* predators (Miranda et al., 1998). Research has been carried out under laboratory conditions to assess the suitability of *T. absoluta* for the predator *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae; Ghoneim, 2014). While Syrphidae, despite being reported to be a specialist for Hemiptera, may also prey on eggs and small larvae in other insect groups (Medeiros, Sujii, & Morais, 2009). All the predators are generalists and may exhibit high pest insect predation capacity in a number of agroecosystems (Musser & Shelton, 2003; Symondson, Sunderland, & Greenstone, 2002).

Hemiptera from the Anthocoridae and Miridae families have also been reported to be predators of different leaf miners (Arno, Alonso, & Gabarra, 2003; Legaspi, French, Zuñiga, & Legaspi, 2001; Passos et al., 2017). Specifically, in the case of *T. absoluta*, the species already reported were *Nesidiocoris tenuis* Reuter, *Macrolophus pygmaeus* Rambur, *Dicyphus marrocannus* Wagner (Hemiptera: Miridae) and *Nabis pseudoferus* Remane (Hemiptera: Nabidae; Desneux et al., 2010). Although only these species had been previously reported, in this study other predatory pirate bugs were found such as *B. pallescens*, *O. tricolor*, *A. constrictus*, *A. bimaculate* and *H. insignis* (Queiroz, Ramos, Gontijo, & Picanço, 2015). These predators were observed in high frequency on tomato leaves from which eggs disappeared and were also observed attacking *T. absoluta* larvae. These Hemiptera may have migrated from weeds present in the growing area searching for food or oviposition sites. The Hemiptera species found in this study may be potential biological control agents for *T. absoluta* (Calvo, Lorente, Stansly, & Belda, 2012; Sylla, Brévault, Diarra, Bearez, & Desneux, 2016). Additionally, other predators such as predatory wasps (*B. lecheguana*, *P. scutellaris* and *P. sylveirae*) were observed attacking 3rd- and 4th-instar *T. absoluta* larvae, whereas ants such as *Solenopsis* sp. were observed attacking pupae. The predatory wasps have been considered efficient natural control agents for larvae from several species and other Lepidopteran pests (Gonring et al., 2003; Picanço et al., 2010), including *T. absoluta* (Picanço et al., 2011). Ants are also predators commonly associated with leaf miners (Urbaneja, Muñoz, Garrido, & Jacas, 2004; Xiao, Qureshi, & Stansly, 2007). As a *T. absoluta* predator, the ants already reported were *Pheidole* sp. (Hymenoptera: Formicidae), *Solenopsis saevissima* Smith (Hymenoptera: Formicidae) and *Solenopsis geminate* (Fabricius) (Hymenoptera: Formicidae; Desneux et al., 2010; Miranda et al., 1998).

Parasitoids observed were *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae), *Bracon* sp., *Earinus* sp., *Pseudapanteles* sp. (Hymenoptera: Braconidae) and *Conura* sp. (Hymenoptera: Chalcididae). Although parasitoids action has not been the most important mortality factor, considering all the periods evaluated, they were present in all the periods, with greater expression in the fall and winter periods and in the 3rd- and 4th-instar larval. Various predators and parasitoids have been reported naturally attacking *T. absoluta* in tomato crops in Europe and North Africa and more recently in India and South America (Biondi, Desneux, Amiens-Desneux, Siscaro, & Zappalà, 2013; Calvo, Soriano, Stansly, & Belda,

2016). Some efforts have targeted the activity of the *T. absoluta* egg (Cabello et al., 2012; Chailleux et al., 2012; El-Arnaouty et al., 2014; Martins et al., 2017) and larval parasitoids (Biondi et al., 2013; Chailleux, Desneux, Arnó, & Gabarra, 2014). However, the most cost-effective and successful biological control programmes are those based on the augmentation and/or conservation of Miridae bugs, such as the omnivorous *M. pygmaeus* and *N. tenuis*, employed alone or in combination with parasitoids (Chailleux, Biondi, Han, Tabone, & Desneux, 2013; Chailleux, Bearez, et al., 2013; De Backer et al., 2015; Naselli et al., 2017) or with selective pesticides (Zappala et al., 2012).

The identification of the critical mortality stages, as well as the mortality factors that act during these stages, have direct implications for pest management. In the dry season, when *T. absoluta* normally presents high population density, pest management programmes could be planned to focus on the key mortality factor responsible for regulating population dynamics during this season. Since natural enemies are the most important factor, conservative biological control would be a strategy to consider. Thus, the population level of natural enemies should be considered during control decision making, to preserve or increase the beneficial action of these organisms in tomato agroecosystems. Therefore, when insecticide use is necessary, selective insecticides should be prioritized to avoid a reduction in natural enemies, as well as the key factors mortality for *T. absoluta* as the predators and parasitoids (Bacci et al., 2009, 2012). Predators and parasitoids were key mortality factors during spring–summer and fall–winter, respectively. Seasonal variation and natural enemies and their attack intensity suggested a strong potential for the use *T. absoluta* as a food and climatic influence on its abundance as was evidenced by the correlation between these climatic factors and the occurrence of these natural enemies (Figure 6).

The poor formation of pupae due to physiological disturbances during winter in the first year was a key mortality factor for *T. absoluta*. The occurrence of this factor may be related to the seasonal variation in climatic elements and their possible effects on the plant quality as a food source for phytophagous insects. Climatic variability may affect metamorphosis regulation by causing changes in the neural and hormonal messengers of the insects (Chapman, 1998). On the other hand, seasonal variations lead to changes in nutritional status and quantity of allelochemicals present in the plant that may cause mortality and physiological disturbances in phytophagous insects (Awmack & Leather, 2002; Chapman, 1998). However, it should be considered that in other times of year, death occurred due to physiological disturbances, despite not being important to regulate *T. absoluta* population dynamics. Although the factors related to the host plant reduce the survival of phytophagous insects, this was not detected directly in ecological life-table studies, which implies an underestimation of the bottom-up effect. Nevertheless, mortality from this effect was evident in the initial larval stages of phytophagous insects (Cornell & Hawkins, 1995). The unknown mortality factor in first-instar *T. absoluta* larvae may possibly be

associated with the characteristics of the host plant. Therefore, the influence of host plant characteristics on *T. absoluta* survival and fecundity is issues that should be investigated in detail in future studies.

The relationship between the occurrence of natural enemies and climatic variations associated with *T. absoluta* mortality showed that predation was higher during the periods of increased temperature, photoperiod and incidence of rainfall (summer and spring), in comparison with parasitism (Figure 6). Other studies have also shown a greater action by predators during summer and parasitoids in winter (Pereira et al., 2007; Semeão et al., 2012). The temporal division in natural enemy occurrence could be associated with physiological adaptations of parasitoids to lower temperatures or due to competition between species of the same trophic level that could interact by intraguild predation (Janssen, Pallini, Venzon, & Sabelis, 1998; Kennedy, 2003; Polis, Myers, & Holt, 1989), resulting in a reduction in control agent efficiency.

In summary, in this study, it was found that *T. absoluta* mortality caused by natural control factors was high and variable throughout the seasons. The critical mortality stage was the larval stage, with final-instar larvae being more vulnerable to natural control factors. The key mortality factor during spring–summer seasons was predation, and in fall–winter, it was parasitism and physiological disorders. Finally, the results showed the importance of the vertical and horizontal action of natural mortality factors.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

Leandro Bacci and Marcelo Coutinho Picanço conceived and designed research. Leandro Bacci, Ézio Marques da Silva, Júlio Cláudio Martins and Mateus Ribeiro Campos contributed to conduction experiments and acquisition of data. Leandro Bacci, Júlio Cláudio Martins and Marcelo Coutinho Picanço analysed data. Leandro Bacci, Júlio Cláudio Martins, Marianne A. Soares and Mateus Ribeiro Campos wrote the manuscript. All authors read, reviewed and approved the manuscript.

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