Research Article

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Natural mortality factors of tomato leafminer *Tuta absoluta* in open-field tomato crops in South America

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Abstract

BACKGROUND: Little importance has been given to the role of natural mortality factors (biotic and abiotic) in the regulation of tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae) populations. The present study determined the action of mortality factors on *T. absoluta* populations infesting cultivated tomato crops. Eighty ecological life tables for *T. absoluta* in field cultivated tomato plants were constructed and analyzed.

RESULTS: Total *T. absoluta* mortality was 99.08%, with 38.76% mortality during the egg phase, 57.20% in the larva phase and 3.12% in the pupal phase. The main mortality factors during the egg stage were predation, parasitism and egg inviability. In the larval stage, the main mortality factors were predation, parasitism, entomopathogenic agents and physiological disorders. In the pupal stage, the main mortality factor was predation. The larvae of the third and fourth instar were more susceptible to the action of mortality factors and the predatory wasp, *Protonectarina sylveirae*, was the main insect predator of these larvae.

CONCLUSIONS: The *T. absoluta* population is regulated under field conditions by the action of natural enemies of the larvae. The predatory wasp *P. sylveirae* is very important in the regulation of *T. absoluta* populations in open-field tomato crops in Brazil.

Keywords: ecological life table; tomato leafminer; natural enemy; critical phase

1 INTRODUCTION

The tomato leafminer *Tuta absoluta* (Polvony) (Lepidoptera: Gelechiidae) is currently the main lepidopteran pest of tomatoes (*Solanum lycopersicum* L.) worldwide. This is due to the damage it causes to leaves, shoots, flowers, and fruits of tomato plants[1–3] and its high capacity for dispersal.[4] It was first documented in Brazil at the beginning of the 1980s and is now prevalent in all states of the country.[2,5] A similar phenomenon occurred in Europe where *T. absoluta* was first reported in Spain in 2006, and has since spread to many other countries in Europe, Africa and Asia.[4,6–8]

Tuta absoluta larvae are leafminers and bore into the branches and fruits of solanaceous plants.[9,10] Within these structures, the larvae are less exposed to natural enemies, climatic elements and insecticides. The endophytic behavior of the larvae decreases the effectiveness of insecticides, because many insecticides present low levels of translocation in tomato plants.[2,11] Brazilian farmers carry out around 60 to 80 insecticide applications per season in an attempt to control *T. absoluta* in tomato crops grown in the field. Despite this heavy insecticide use, failure to control this pest has been observed in several tomato producing regions. The main causes of this failure are selection for insecticide resistant populations, the impact of pesticides on natural enemies and poor spray technology.[12,13]

A lack of knowledge concerning the role of natural enemies (top-down force), climatic factors and plant defenses (bottom-up force) in insect pest population dynamics can lead to farmers focusing on insecticide use as the main mechanism for reducing insect pest populations in crops, while overlooking the importance of natural factors. Several indigenous enemies were reported in tomato crops which cause mortality of *T. absoluta*. In particular, insects predators (Coccinellidae, Formicidae, Miridae, Nabidae and Vespidae), parasitoids (Braconidae, Elasmidae, Eulophidae, Ichneumonidae, Pteromalidae and Trichogrammatidae) and entomopathogenic microorganisms.[4,7,14–18]

Natural mortality factors help to regulate pest populations, reduce losses caused by pests in crops, are environmentally safe

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and have little or no impact on production costs.[19] Ecological life tables can provide important information about the mortality factors affecting insect population dynamics, allowing the identification and quantification of mortality caused by specific factors and the life-stages that determine insect pest population size.[14,20–23] Mortality factors may act during all insect life-stages, with the eggs and immature stages being the most susceptible.

The present study was designed to investigate the impact of natural mortality factors on a *T. absoluta* population by building ecological life tables. We carried out the experiments in a major tomato producing region of Brazil. Mortality factors were checked daily, beginning at sunrise and ending at sunset. The results obtained will be very important for the planning of future integrated pest management programs.

2 MATERIAL AND METHODS

This study was carried out in the experimental area of the Federal University of Viçosa (20°48′45″S; 42°56′15″W; altitude 672 m; tropical climate), in the State of Minas Gerais, Brazil. The *S. licopersicum* variety of tomato, locally known as 'Santa Clara,' was used. Tomato plants were cultivated in open fields during 2 years, the interval between tomato planting was 3 months. Each crop occupied a total area of 864 m^2 and this area was divided into four blocks (180 m^2). Each block consisted of 12 rows of plants, containing 30 tomato plants with a spacing of 0.5 m between plants and 1 m between rows. Standard agronomic practices for tomatoes were applied to all blocks, with pesticide spraying for insect and disease control not carried out.

2.1 Cohort establishment

The insects used in this study were from a *T. absoluta* colony maintained in the Integrated Pest Management Laboratory of the Federal University of Viçosa. Thirty *T. absoluta* adults (2 days old) were caged with tomato plant branches using netting bags (size: 30 cm × 40 cm). After a 24 h period, most of the adults had died and the bags were removed and any surviving adults were killed by crushing. The egg cohorts were quantified and mapped through the schematic drawing of tomato leaves. The number of eggs per plant was 150 and any excess eggs were removed using a brush (size 1).

Egg mortality was calculated from the number of *T. absoluta* eggs originally laid on the leaves when compared to the number of 1st instar larvae. The second, third and fourth larval stages were obtained from the laboratory colony [25 ± 0.5 °C, relative humidity (RH) 75 ± 5% and photoperiod 12 h:12 h (light/dark, *L/D*)] which had been maintained on tomato plants (Santa Clara variety) and transferred with a brush to a leaf in the middle portion of each tomato plant in the field. A total of 25 larvae of each instar (five larvae per leaf) were transferred to tomato plants. This density is in agreement with that observed naturally in the field.[24]

For pupal life tables, 30 pupae from the laboratory colony were placed in plastic pots (10 cm diameter × 7 cm high), filled with sand, and then the pupae were covered with a thin layer of sand. The pots were then buried next to the base of the tomato plants, such that the top edge of the pot was at ground level. The pots were maintained in the field for 6 days.[25]

2.2 Assessment of mortality factors in field conditions

Natural mortality of *T. absoluta* eggs, larvae, and pupae was monitored daily from 6:00 to 18:00 h. The mortality in the field caused by predators and rainfall was determined. Mortality resulting from parasitism, entomopathogens (fungi, bacteria, or viruses), egg inviability, and physiological disturbances (larvae that died showing signs of predation and disease symptoms) were determined in the laboratory. Dead larvae with signs or symptoms of fungal and bacterial diseases were evaluated according to symptomatology.[18] Samples from diseased larvae were collected and taken to the laboratory and placed in Petri dishes (diameter of 9 cm) containing specific culture medium for each pathogen group. Egg and larval mortality caused by rainfall was determined by the difference in egg numbers and living larvae before and after each rainfall.[23] Mortality caused by rainfall was recorded immediately after the event, through the observation of the presence of water inside the mine. Eggs that disappeared between two consecutive evaluations were considered to have been subject to predation.[18,23] The presence of putative predators on each leaf was recorded, and specimens were collected and maintained in Eppendorf tubes containing 70% ethanol for subsequent identification.

Eggs that did not hatch were transferred to test-tubes to observe the possible emergence of parasitoids or the occurrence of egg inviability.

The first, second, third and fourth instar larvae that survived to the end of the larval developmental stage were taken to the laboratory and transferred to tomato leaves for observation of *T. absoluta* adult emergence or possible parasitoid emergence. Pupal predation frequencies were calculated from the difference between the initial number of pupae placed in the pots and the number of pupae remaining at the end of the experiment. The remaining pupae were transferred to test tubes and placed in a temperature and humidity controlled environment [25 ± 0.5 °C, RH 75 ± 5% and photoperiod 12 h:12 h (*L:D*)] for 30 days to observe the emergence of *T. absoluta* adults and parasitoids. The pupae that did not become adults and that had not been parasitized, were classified as dead from the effects of rainfall or possible physiological disorders.

Parasitoid specimens were identified by Dr Angélica Maria Penteado Martins Dias of the Federal University of São Carlos, Brazil. Hemipteran predators were identified by Dr Paulo Sérgio Fiuza Ferreira and fungi were identified by Dr Simon Luke Elliot, both from the Federal of University of Viçosa (UFV), Brazil. Coleopteran predators were identified by Dr Ayr de Moura Bello.

2.3 Analyses of life tables

Tuta absoluta life tables were constructed using the methodology of Southwood and Henderson.[26] The life tables presented *T. absoluta* developmental stages and mortality factors, number of individuals at the start of the experiment (lx), mortality at each stage (dx) and the apparent percent mortality (100qx). The 100qx was calculated by the formula:

$$100qx = \left[dx/lx\right]/100$$

where l_0 = number of eggs at the beginning of the life table evaluation; l_0 was transformed to 10 000.

The net reproductive rate (R_0) was obtained by dividing the number of expected eggs in the next generation (number of adult survivors in the actual cohort × sex ratio × adult fertility) by the total number of eggs (10 000) present at the beginning of each cohort. We considered the sex ratio as equal to 0.5973 and fecundity as 183 eggs/female.[27]

The critical phase, critical stage and key mortality factors of *T. absoluta* were determined by correlation and linear regression analyses using specific stage mortality (k) and total mortality ($K = Pk$) at $P < 0.05$. The value of k was obtained by the formula $k = \log(100qx)$. The critical phase, critical stage and key mortality factors were considered as those which presented a significant correlation ($P < 0.05$) with total mortality, producing a regression curve showing the highest inclination coefficient ($P < 0.05$), and having the greatest similarity (R^2) with total mortality.[18,23,25,26]

3 RESULTS

During the observation of 80 *T. absoluta* generations, we found that for 10 000 eggs only 91.28 ± 18.39 resulted in adults. This represents a survival rate of only 0.92%. The apparent mortality rates for the egg, larval and pupal stages were 38.76, 93.41 and 77.4%, respectively. During the first, second, third and fourth instar larval stages, mortality was 36.66, 40.82, 63.04 and 52.40%, respectively. The population growth rate was approximately one ($t_{1,158} = 0.012$, $P = 0.99$).

Several factors contributed to *T. absoluta* mortality at different life stages. Coleoptera, Hemiptera, Hymenoptera, Neuroptera and spiders (Araneae) were observed to be predators of immature stages of *T. absoluta*. The principal predators observed were the beetle *Oxypodini* sp. (Coleoptera: Staphylinidae), bugs of the genus *Orius* sp., *Lasiochilus* sp. (Heteroptera: Anthocoridae), *Annona bimaculata* Distant, and *Hyaliodocoris insignis* (Stal.) (Heteroptera: Miridae). The main Hymenopteran predators were the wasps *Brachygastra lecheguana* (Latr.), *Polybia scutellaris* (White), *Protonectarina sylveirae* (Saussure) (Hymenoptera: Vespidae) and predatory ants of the genus *Solenopsis* sp. (Hymenopetra: Formicidae). In the order Neuroptera, the main representative predators were green lacewing larvae of the genus *Chrysoperla* sp. (Chrysopidae) (Table 1).

The most important parasitoids were *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) for eggs, *Bracon* sp. and *Earinus* sp. (Hymenoptera: Braconidae) for third and fourth instar larvae and *Pseudapanteles* sp. (Hymenoptera: Braconidae) for pupae (Table 1).

3.1 Phase and critical stage for *T. absoluta* mortality

The larval mortality curve was unique showing the greatest similarity to total mortality of *T. absoluta* ($r = 0.98$; $P < 0.001$) (Fig. 1(A)). The larval mortality curves of the second ($r = 0.75$; $P < 0.001$), third ($r = 0.93$; $P < 0.001$) and fourth ($r = 0.92$; $P < 0.001$) instars correlated significantly with total larval mortality (Fig. 1(B)). The curves for third and fourth instar larvae showed higher angular coefficients and were the most highly correlated with total mortality of the larval stage. The overlapping confidence intervals of their angular coefficients demonstrated that the mortality curves of third and fourth instar larvae were statistically similar (Fig. 1(C)). The critical phase of *T. absoluta* was shown to be the larval stage and the critical stages for mortality were third and fourth instar larvae. The key mortality factor was predation and the critical component of this mortality was predation by the wasp *P. sylveirae*.

3.2 Key-factors and critical components of *T. absoluta* mortality

In third ($r = 0.95$; $P < 0.001$) and fourth ($r = 0.90$; $P < 0.001$) instar larvae, only mortality caused by predation correlated significantly with the total mortality (Figs 2(A) and 3(A)). Predation by the wasp *P. sylveirae* was the main mortality component during the third and fourth instars. The mortality curve observed as a result of *P. sylveirae* predation significantly correlated with total predation observed during these instars (Figs 2(B) and 3(B)).

In summary, the critical phase of the *T. absoluta* life cycle was the larval stage, and within that stage the critical stages were the third and fourth instar larval stages. The key mortality factor was predation and the critical mortality component was predation by the wasp *P. sylveirae*.

4 DISCUSSION

The information generated by this study demonstrated the importance of biotic and abiotic factors in regulating *T. absoluta* population dynamics. Knowledge of these factors is essential for the implementation of integrated pest management programs for the control of *T. absoluta* in tomato crops.

The population of *T. absoluta* remained constant over 80 generations ($R_0 = 1$) in tomato plants. This equilibrium was the result of climatic factors and bottom-up and top-down factors affecting the pest population dynamics. The observation of the action of bottom-up factors in herbivores is most evident in non-domesticated plants.[28] The defense compounds of tomato plants may have been responsible for unviable eggs and the physiological disorders seen in larvae and pupae. These compounds can act on the physiological processes of insects, either reducing their biological performance or causing mortality.[29,30]

The top-down factors were the most important in reducing the *T. absoluta* population. These factors are important in the population dynamics of arthropod pests in agro-ecosystems.[14,18,31] In these situations, the simplification of environmental factors in monocultures creates favorable conditions for the establishment of phytophagous insect populations in host plants. By contrast, the high population density of phytophagous insects may support the occurrence and maintenance of natural enemies (predators, parasitoids and entomopathogens).[18,23,32–34]

Third and fourth instar larvae were shown to be the critical stages for *T. absoluta* mortality. These results are different from those obtained by Miranda *et al.*,[14] where the critical stages for *T. absoluta* were found to be the first and second instar larval stages. Miranda *et al*[14] applied insecticides during the study with smaller larvae being more susceptible to insecticides than larger larvae. This was probably due to their higher specific surface area resulting in greater exposure to these products. Additionally, insecticides are likely to have an adverse effect on *T. absoluta* natural enemies,[35] masking the action of these organisms in larger larvae. Larger larvae represent a greater reward for predators and are easier to find on plants than smaller larvae.[36] Corroborating our results, Gonring *et al.*[33] observed that third and fifth instar larvae were the critical mortality stages for *Diaphania nitidalis* and the key mortality factor was predation by the wasp *Polybia ignobillis*. Although leaf mining behavior protects *T. absoluta* larvae from the action of natural enemies, confinement in these spaces may leave larvae vulnerable to the action of natural enemies that are capable of locating the larvae inside the mines and breach the protection of the mine to prey on the larva. The predation of larger larvae in open-field tomato crops has also been reported in Iran, Spain, Egypt, Jordan, France, Israel, Turkey, Marocco, Italy and Tunisia, countries where *T. absoluta* is considered an invasive pest.[37,38]

Ecological life tables provide important information about the factors that regulate the population dynamics of phytophagous insects.[18,22,23] Using this tool, it is possible to identify the critical phase and main factors that cause insect mortality in the environment.[19] Although mortality factors may act on all

Table 1. Ecological life table for *Tuta absoluta* in tomato plants, Viçosa county, State of Minas Gerais

Stages/mortality factors	Lx	dx	100qx
Eggs	10 000.00 ± 0.00	3876.24 ± 183.88	38.76 ± 1.84
Rainfall		502.12 ± 82.28	5.02 ± 0.82
Predation		1603.40 ± 138.05	16.03 ± 1.38
Parasitism		818.44 ± 126.25	8.19 ± 1.26
Trichogramma sp.		818.44 ± 126.25	8.19 ± 1.26
Inviability		952.28 ± 95.48	9.52 ± 0.95
First instar larva	6123.76 ± 183.90	2244.72 ± 179.66	36.66 ± 1.80
Rainfall		228.69 ± 37.55	3.74 ± 0.38
Predation		1843.81 ± 148.46	30.11 ± 1.48
Physiological distubance		172.22 ± 32.40	2.81 ± 0.32
Second instar larva	3879.05 ± 165.34	1583.49 ± 144.05	40.82 ± 1.44
Rainfall		0.00 ± 0.00	0.00 ± 0.00
Predation		1544.03 ± 144.10	39.80 ± 1.44
Bugs predators		691.20 ± 63.88	17.82 ± 0.64
Protonectarina sylveirae		846.42 ± 154.09	21.82 ± 1.54
Chrysoperla externa		6.41 ± 6.41	0.17 ± 0.06
Physiological disturbance		26.48 ± 9.46	0.68 ± 0.09
Pathogens		12.98 ± 8.66	0.33 ± 0.09
Bacteria		1.65 ± 1.65	0.04 ± 0.02
Fungi		11.33 ± 8.53	0.29 ± 0.09
Third instar larva	2295.56 ± 153.92	1447.22 ± 116.94	63.06 ± 1.17
Rainfall		133.98 ± 32.16	5.84 ± 0.32
Predation		890.14 ± 115.62	38.78 ± 1.16
Bugs predators		13.23 ± 6.64	0.58 ± 0.07
Protonectarina sylveirae		872.32 ± 114.84	38.00 ± 1.15
Brachygastra lecheguana		3.40 ± 2.47	0.15 ± 0.02
Spiders		1.20 ± 0.87	0.05 ± 0.01
Physiological disturbance		32.52 ± 13.76	1.42 ± 0.14
Diseases		17.18 ± 7.65	0.75 ± 0.08
Bacteria		13.00 ± 7.40	0.57 ± 0.07
Fungi		4.18 ± 2.26	0.18 ± 0.02
Parasitism		373.40 ± 74.66	16.27 ± 0.75
Bracon sp.		371.79 ± 74.67	16.20 ± 0.75
Earinus sp.		1.61 ± 1.13	0.07 ± 0.01
Fourth instar larva	848.34 ± 106.40	444.55 ± 53.26	52.41 ± 0.53
Rainfall		19.81 ± 5.30	2.34 ± 0.05
Predation		180.74 ± 34.88	21.31 ± 0.35
Bugs predators		3.90 ± 2.39	0.46 ± 0.02
Protonectarina sylveirae		174.12 ± 34.31	20.53 ± 0.34
Brachygastra lecheguana		0.48 ± 0.33	0.06 ± 0.00
Polybia scutellaris		0.54 ± 0.38	0.06 ± 0.00
Oxypodini sp.		1.56 ± 1.56	0.18 ± 0.02
Spiders		0.13 ± 0.13	0.02 ± 0.00
Physiological disturbance		10.75 ± 4.26	1.27 ± 0.04
Diseases		8.55 ± 3.28	1.01 ± 0.03
Bacteria		1.23 ± 1.18	0.14 ± 0.01
Fungi		7.33 ± 3.09	0.87 ± 0.03
Parasitism		224.70 ± 44.32	26.49 ± 0.44
Bracon sp.		218.80 ± 43.94	25.79 ± 0.44
Earinus sp.		5.90 ± 3.28	0.70 ± 0.03
Conura sp.		0.001 ± 0.001	0.00 ± 0.00

Table 1. Continued

Stages/mortality factors	Lx	dx	100qx
Pupa	403.80 ± 73.85	312.52 ± 58.87	77.39 ± 0.59
Rainfall		3.77 ± 2.60	0.93 ± 0.03
Predation		227.03 ± 43.89	56.22 ± 0.44
Formicidae		227.03 ± 43.89	56.22 ± 0.44
Physiological disturbance		76.42 ± 21.77	18.93 ± 0.22
Parasitism		5.30 ± 2.72	1.31 ± 0.03
Pseudapanteles sp.		5.30 ± 2.72	1.31 ± 0.03
Adults	91.28 ± 18.39		
Total mortality	99.08%		
R_0	0.99 ± 0.19		

In the table, lx corresponds to the number of insects alive at the beginning of each stage (± standard error), dx is the number of insects killed by a factor (± standard error) for each stage, 100qx is the apparent mortality percentage or the percentage of insects killed by a factor during a specific life stage and R_0 is net reproductive rate.

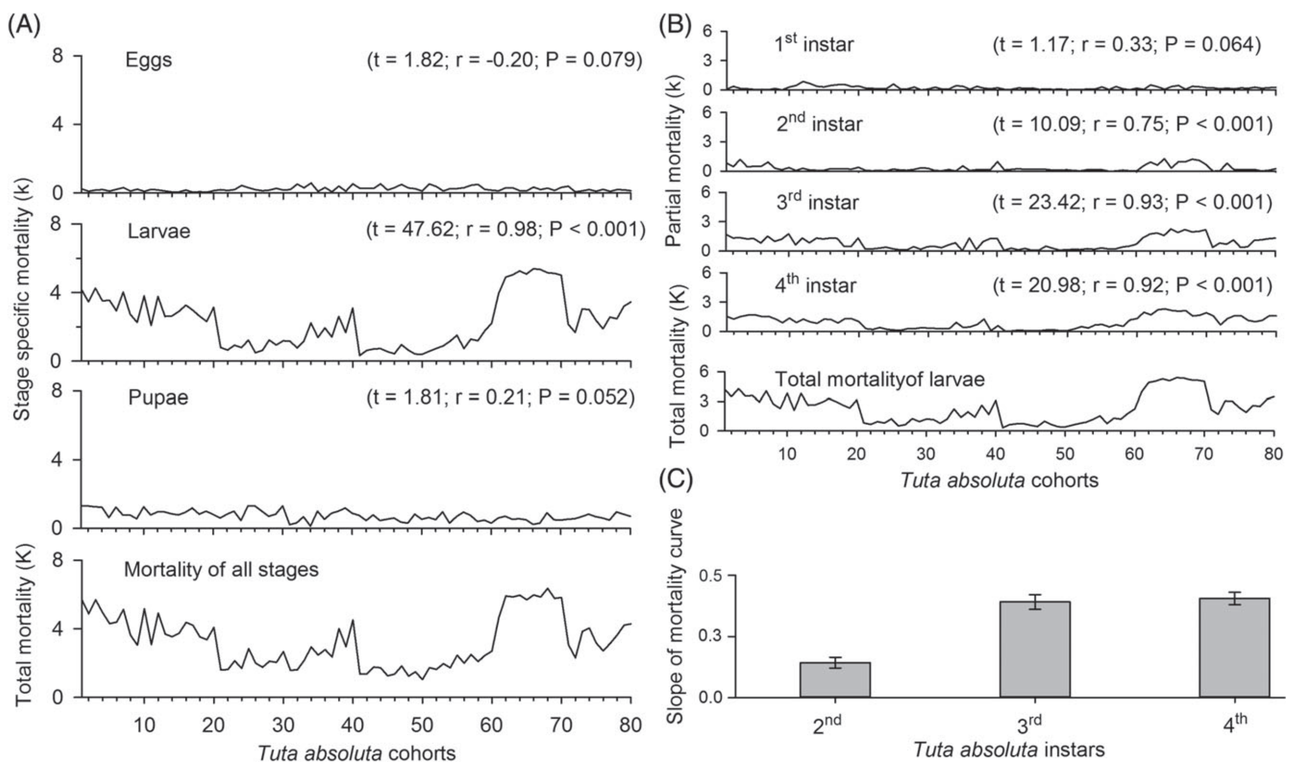

Figure 1. Determination of the critical phase and critical stage for *Tuta absoluta* mortality: (A) correlation of mortality at each *T. absoluta* life stage with total mortality of all immature stages combined; (B and C) correlations and regression curves of mortality of larvae in the first, second, third and fourth instar larval stages with total mortality. The confidence intervals for each regression curve were calculated at 95% probability.

immature stages of insects, our results show a higher vulnerability of the larval stage to the action of these factors. The *T. absoluta* larval period is longer (8–32 days) than the egg phase (4–8 days) or the pupal phase (4–18 days).[39] Thus, the larval stage presents greater risk of mortality due to longer exposure to mortality factors. These results corroborate with studies by Pereira *et al.*[18] and Gonring *et al.*[33] These authors found higher susceptibility of the larval stages of *Diaphania* sp. and *Leucoptera coffeella* to natural mortality factors in cucumber and coffee crops, respectively.

Another important mortality factor for the insect was rainfall. Rainfall can cause egg and larval mortality due to mechanical damage from the impact of the rain drops or by drowning. Insects that are endophytic can be killed by drowning due to flooding of mines by rainfall, the entry and accumulation of water is proportional to the size of the mine. Third and fourth instar *T. absoluta* larvae create large mines in tomato leaves and therefore may be more vulnerable to death by drowning.

Predatory wasps were a critical mortality component for third and fourth instar larvae. Larger larvae have higher body mass and may be more compensatory to these wasps. The high predation exerted by Vespidae may be due to previous experience, distribution and abundance of prey.[36] Social wasps can be opportunistic and generalist predators that often return to hunt at sites that presented previous hunting success and may feed repeatedly on the

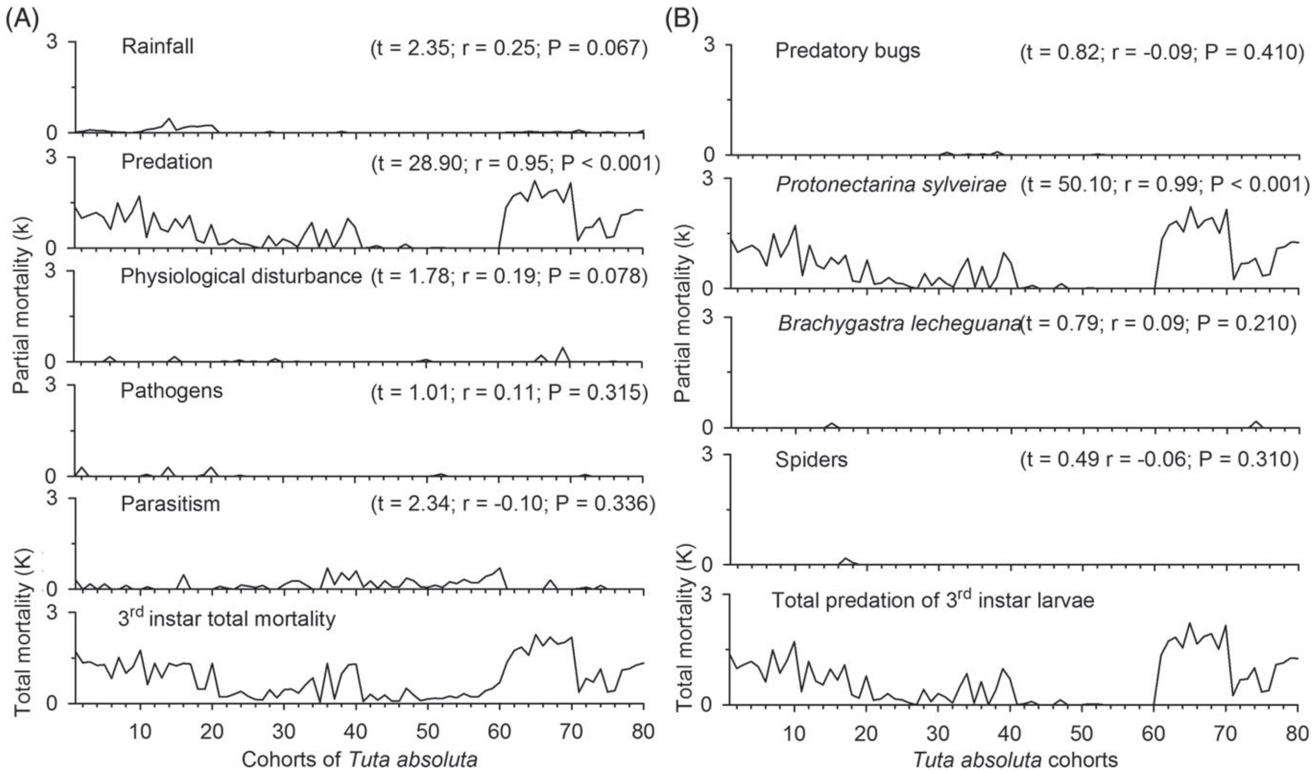

Figure 2. Determination of the key mortality factors occurring during the third instar larval stage of *Tuta absoluta*: (A) correlation between mortality factors and total mortality; (B) correlations of mortality caused by specific predators with total predation. The confidence intervals for each regression curve were calculated at 95% probability.

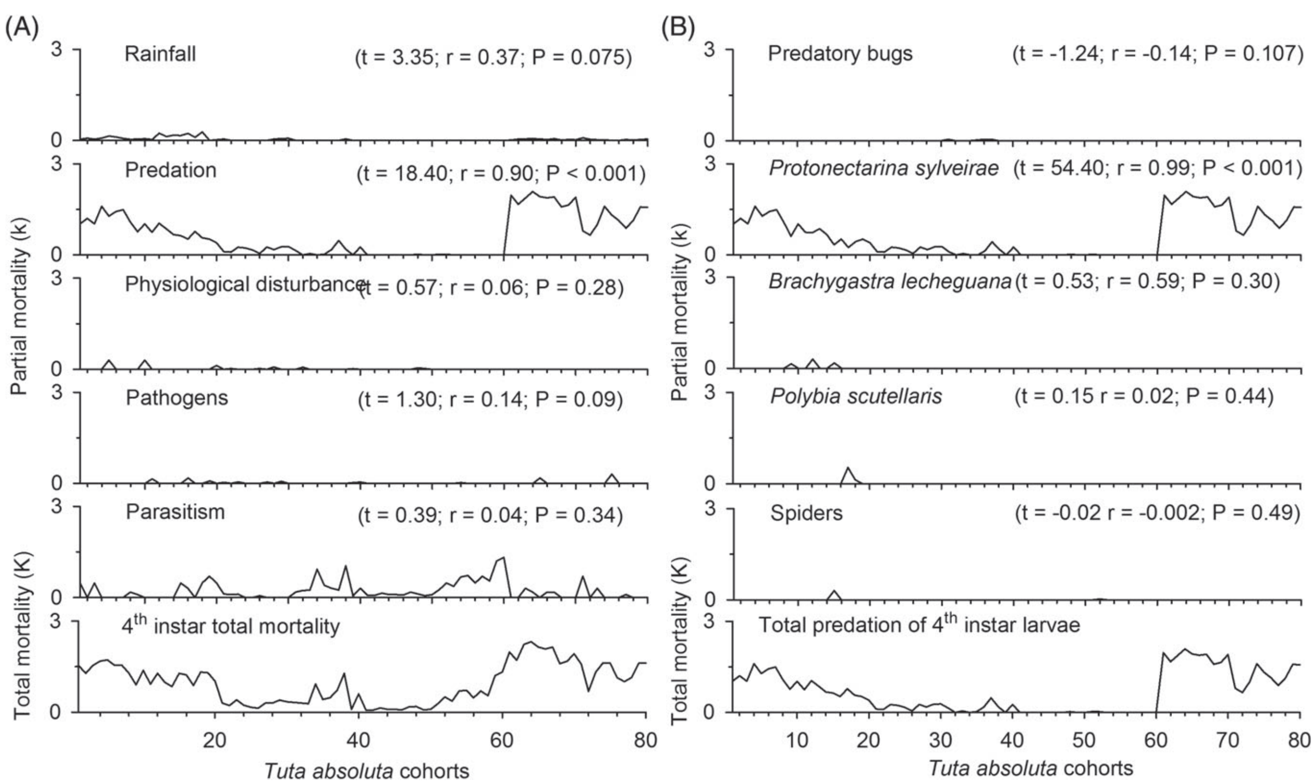

Figure 3. Determination of key mortality factors for fourth instar larvae of *Tuta absoluta*: (A) correlation between mortality factors and total mortality; (B) correlations of mortality caused by specific predators with total predation. The confidence intervals for each regression curve were calculated at 95% probability.

same species of prey, behaving as facultative specialists. Therefore the success of foraging increases with age and experience of the wasp.[40–42] The high predation rate exerted by *P. sylveirae* could also be related to the distribution and frequency of wasp nests in the locality where we carried out this study. *Protonectarina sylveirae* has a broad geographic distribution throughout South America, from Brazil to Argentina, although it is not found in the Amazon region of Brazil. This species builds very large and perennial arboreal nests and form colonies with large populations.[43–45] In Brazil, the sites of open-field tomato crops used here coincided with the occurrence of *P. sylveirae* colonies.[2,46] At other sites or in other countries, different natural enemies and other environmental factors may play a role in *T. absoluta* population regulation.[37,38]

The physical characteristics of the plant can also affect foraging by natural enemies.[46] The size, architecture, leaf area, and trichomes of the host plant (glandular and non-glandular) may alter searching efficiency and capture of the pest by natural enemies. Natural enemies take more time to find prey in plants with complex architecture (highly branching) than with simple architecture.[47–49] Tomato plants have a simple architecture which appears not to negatively affect the foraging success of natural enemies.

Host plant volatile compounds may have a direct effect on pest and natural enemy behavior. Studies have demonstrated that volatile compounds released by damaged plants can attract arthropod natural enemies of herbivores.[50,51] Predatory wasps prefer to forage on plants damaged by insects rather than on undamaged plants, while wasps may also mark plants or leaves to help in prey localization.[48]

In this context, the adoption of practices that contribute to increasing the diversity of agroecosystems is important to conserve and enhance natural enemy populations. Therefore, insecticides which are less toxic to natural enemies should be chosen to control *T. absoluta*. Furthermore, these products should be used at times when natural enemies are less active in the field, especially considering that predatory wasps are more active foraging in tomato fields between 10:00 and 16:00 h.[23,52,53]

In conclusion, we found that natural control factors are important in the regulation of *T. absoluta* populations in tomato fields. The critical phase of the life cycle is the larval phase and the critical stages are the third and fourth instars. Predation by wasps is a very important mortality factor and is fundamental for the natural management of *T. absoluta* populations in tomato fields. Control strategies need to take into account these findings, in order to reduce pest populations without the random application of insecticides, as is the current scenario in Brazil.

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