



Thermal biology of *Tuta absoluta*: demographic parameters and facultative diapause

Mateus Ribeiro de Campos¹ · Philippe Béarez¹ · Edwige Amiens-Desneux¹ · Luigi Ponti^{2,3} · Andrew Paul Gutierrez^{3,4} · Antonio Biondi⁵ · Abhijin Adiga⁶ · Nicolas Desneux¹

Received: 9 June 2020 / Revised: 4 September 2020 / Accepted: 21 September 2020 / Published online: 6 October 2020
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

Abstract

The South American tomato pinworm, *Tuta absoluta*, (SATP) is now a devastating pest worldwide of crops in the family Solanaceae. Most prior studies of SATP's thermal biology were based on populations from tropical regions, and proved unsuitable for explaining its invasion of large areas of the Palearctic. A more holistic approach to the analysis of its thermal biology is essential background for developing models to assess its invasive potential. Our studies found that SATP has lower and upper thermal thresholds ($\theta_L = 5.37^\circ\text{C}$ and $\theta_U = 35.69^\circ\text{C}$, respectively) than South American populations used in prior studies ($\theta_L = 7.38^\circ\text{C}$ and $\theta_U = 33.82^\circ\text{C}$). Age-specific life tables were used to estimate the effects of temperature on its demographic parameters. Diapause in SATP had not been characterized prior to our study. We found facultative diapause in pupae developing from larvae exposed to relatively low temperatures (i.e., 2 and 5 °C) and short-day length for different exposure periods. The strength of diapause was measured as an increase in post-treatment developmental times of pupae (i.e., degree days) that on average were 2.45–3-fold greater than of pupae reared at favorable temperatures. A lower developmental threshold and a facultative diapause increase the invasive potential of SATP in temperate areas. Knowledge of this thermal biology is essential for predicting the potential geographic spread of this pest and to develop management and control strategies.

Keywords Invasive pest · Thermal biology · Temperature thresholds · Diapause · Phenotypic plasticity · Geographic variation

Abbreviations

SATP	South American tomato pinworm
θ_L	Lower temperature threshold
θ_U	Upper temperature threshold
R_0	Net reproductive rate
λ	Finite rate of increase
r_m	Intrinsic rate of increase
τ	Generation time
K	Degree-day
T	Temperature
dl	Minutes day length
E	Exposure periods

Key messages

- Demographic parameters estimated at different temperatures show that *T. absoluta* has a rapid developmental time and can reproduce at temperatures close to the development threshold.
- *T. absoluta* from a temperate region (France) has a lower temperature threshold for development than strains from tropical regions in South America, but this awaits independent confirmation as it has important ecological implications for its invasive capacities.
- Facultative diapause in *T. absoluta* was confirmed experimentally in response to low non freezing temperatures, day length and exposure periods.

Communicated by M. Traugott.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10340-020-01286-8>) contains supplementary material, which is available to authorized users.

✉ Mateus Ribeiro de Campos
mateusrcampos@gmail.com

Extended author information available on the last page of the article

Introduction

Exotic invasive species threaten native species and ecosystems globally (Asplen et al. 2015; Lee et al. 2020; Requier et al. 2019; Roques et al. 2016). Among the most important is the highly invasive South American tomato pinworm, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) (SATP), a destructive invasive pest of tomato and other crops in the family Solanaceae worldwide (Biondi et al. 2018; Desneux et al. 2010; Guedes and Picanço 2012). From its native range in the Peruvian central highlands in South America, it reached eastern Spain in 2006, and spread rapidly to Central Europe and Mediterranean countries of Europe and Africa (Mansour et al. 2018; Sylla et al. 2017), and is expanding its range into Asia (Han et al. 2018, 2019). Its current range includes most Central and Southwest Asian countries neighboring China (Biondi et al. 2018; Desneux et al. 2011; McNitt et al. 2019), and threatens to invade important tomato producer-exporter countries such as China and United State (Campos et al. 2017; Han et al. 2019; Verheggen and Fontus 2019).

Sound data on the thermal biology of invasive species such as SATP are essential to developing models to predict the prospective geographic distribution and relative abundance of invasive species under extant and climate change weather, and for the development of integrated pest management (IPM) strategies (Gutierrez 1996; Kang et al. 2009). Temperature is a key factor in the survival, reproduction and abundance of poikilotherms species (Briere et al. 1999; Flitters and Messenger 1965; Gilbert and Gutierrez 1973; Lactin et al. 1995; Logan et al. 1976), but the effects are often not considered (Cherif et al. 2019; Iltis et al. 2020; Martins et al. 2016; Rank et al. 2020).

In this paper, we take a holistic approach to estimate the effects of temperature on the demographic parameters of SATP using age-specific life tables as a basis (Barrientos et al. 1998; Cherif et al. 2019; Krechemer and Foerster 2015; Martins et al. 2016). Life table parameters provide information about the limiting effects of temperature on the vital rates of species (Desneux et al. 2010; Ponti et al. 2015a, b). Ecological niche models based on occurrence data and aggregate weather and biological factors in the species' native range have been used to estimate their potential geographic range (Lawler et al. 2006; Tonnang et al. 2015). Mechanistic physiologically based population dynamics models based on non-linear biodynamic functions of the ecological and biological processes affecting the population dynamics of insects, including diapause (Gutierrez 1996; Gutierrez et al. 2015), can be used to predict and explain the geographic distribution and the relative abundance of species.

Our paper seeks to fill the gaps in the thermal biology of SATP across its wider range of temperatures (Ponti et al. 2015a) and to investigate the occurrence of diapause. Changes

in climatic factors may promote adaptive behavioral and physiological changes in insects such as diapause (Leather et al. 1993) that may be critical components in their life history strategy, enabling survival in unfavorable environmental conditions (Danks 2007; Musolin et al. 2019; Tauber et al. 1986). Diapause may be quiescence, facultative or obligate, and may be induced by environmental stimuli such as temperature, photoperiod and other factors (Denlinger 2002, 2008). Diapause in SATP had not been previously documented (Kahner et al. 2019), though indications of diapause were preliminarily reported by Sannino and Espinosa (2010) in the last summer generation near Salerno, Italy, where 13 of 33 pupae became adults in 17.9 ± 0.41 days, while 20 pupae required 65.1 ± 1.16 days (see Ponti et al. 2015b).

Materials and methods

Growth chamber and greenhouse production of host plants

Pesticide-free tomato plants *cv.* Marmande grown from seed germinated in a climatic chamber at 24 ± 2 °C (*T*), $65 \pm 5\%$ relative humidity (RH), and 16:08 h (Light:Dark, L:D) photoperiod were used as hosts for SATP. After germination, the tomato seedlings were planted in 320-mL plastic pots in a commercial substrate (Tournesol®, Nice, France), and transferred to a greenhouse kept at 20 ± 2 °C, $65 \pm 5\%$ RH, and photoperiod of 10:14 h L:D. The mean daytime global irradiance inside the greenhouse was maintained at 449.5 W m^{-2} using shading as required. The plants were later replanted in 2.8-L pot using inert perlite as a substrate (Perlite Italiana srl, Corsico, Italy), and fertilized with a nutrient mineral solution developed by the French National Institute for Agricultural Research & Environment (INRAe) Sophia Antipolis, France ($\text{NO}_3 = 1 \text{ mol m}^{-3}$; $\text{H}_2\text{PO}_4 = 0.21 \text{ mol m}^{-3}$; $\text{SO}_4 = 0.055 \text{ mol m}^{-3}$; $\text{K} = 0.641 \text{ mol m}^{-3}$, $\text{Ca} = 0.215 \text{ mol m}^{-3}$; $\text{Mg} = 0.114 \text{ mol m}^{-3}$ adjusted to pH 6.0 ± 0.2 using 0.2 M aqueous solution of H_2SO_4) (Han et al. 2014).

Tuta absoluta colonies

Colonies of SATP were established from field adults collected in July 2009 on the INRAe campus, Alénia, France. The colonies were maintained in eight cages ($55 \times 75 \times 80$ cm) as mixed stages (egg, larval, pupal, and adult) on leaves from potted greenhouse tomato plants. The cages were housed in controlled environmental growth chambers maintained at 24 ± 2 °C, $65 \pm 5\%$ RH, and 16:08 h L:D. Large numbers of equal age individuals required for the experiments were obtained by providing adult females with preferred young leaves (Anastasaki et al. 2018) in a cage

for 48 h, and subsets of leaves with eggs were transferred to smaller cages for hatching. Newly hatched larvae were supplied daily with new leaves.

Laboratory cages for estimating vital rates

Small plastic cages each composed of two plastic cups (Biondi et al. 2012) were used in all laboratory experiments to assess the temperature-dependent vital rates, and to assess the effects of temperature (T , °C) \times day length (dl , minutes) \times exposure periods (E , days) on diapause induction. The top cup was 15 cm high with a volume of 700 mL with a one-cm diameter hole drilled in the bottom to allow the insertion of a leaf stem allowing access to water in the second 11 cm high, 350 mL cup. Leaves ~ 50 days of age (15 cm long with seven leaflets) collected from the mid- and upper levels of greenhouse plants were used as hosts for the larvae (Torres et al. 2001). An organdy cloth screen was affixed to the top of the first plastic cup with a rubber band to allow ventilation, and access to determine the development of the experimental insects.

Thermal biology experiments

Forty replicates at each of eight constant temperatures (6, 10, 15, 20, 25, 30, 33 and 36 °C \pm 1, 60 \pm 5% RH, and 16:08 h L:D) were used to estimate developmental times and thermal thresholds of each immature life stage. Each replicate consisted of three first-instar larvae per cage. All experiments were conducted in incubators (model TC445 S, Aqualytic® LIEBHERR, Tintometer GmbH, Austria) using a TFH 620 ebro® Electronic GmbH & Co. KG, Germany sensor to monitor temperatures. The time interval between observations decreased with increasing temperature. At 6, 10, 15, and 20 °C, observations were made every two days, while at 25, 30, 33, and 36 °C observations occurred daily. The temperatures used mirrored the range in previous studies (Barrientos et al. 1998; Krechmer and Foerster 2015; Martins et al. 2016; Ponti et al. 2015a) (Supplementary material, Table S1).

Lifespan and reproduction under winter conditions

On February 21, 2018, large numbers of eggs were collected on new leaves in the laboratory as described above and then transferred to field conditions in 55 \times 75 \times 80 cm screen cages where they remained until adult emergence. Field temperatures recorded by the meteorological station at INRAe were used to assess the effects of temperature on field survival. After emergence in spring, the adults were taken to the laboratory where 40 male–female pair replicates in small cages were maintained at 24 \pm 2 °C, 65 \pm 5%

RH and 16:08 h L:D. Daily oviposition and mortality of the females were recorded.

Life table analysis

The life table data were analyzed using the age-stage, two-sex life table methods (Chi 1988; Chi and Liu 1985). The net reproductive rate (R_0), mean generation time (τ), intrinsic rate of increase (r_m), and finite rate of increase (λ) were calculated using the TWOSEX-MSChart procedure (Chi 2019, Chi et al. 2020). The mean, variance, and standard error of the life table parameters were estimated using 100,000 bootstrap samples (Efron and Tibshirani 1986) for comparison across temperature treatments. Basic age-specific life table data consist of the average age of the insects from egg eclosion (x); the number alive at the beginning of each age (a_x); the proportion surviving to each life stage x (l_x) obtained by dividing the number of individuals living at the beginning of each age (a_x) by the initial number of initial eggs; the number of females produced per female at age x (m_x); the total number of females produced at age x ($l_x m_x$). Generation time (τ) was estimated as $\sum x l_x m_x / l_x m_x$. The intrinsic rate of natural increase (r_m) was estimated by solving the equation $\sum_{x=0}^{\infty} e^{-r_m(x+1)} l_x m_x = 1$ (Goodman 1982). The sex ratio (1:1) was estimated at the pupal stage (Bacci et al. 2019).

Effects of temperature on demographic functions

Rate of development

The developmental rate for each life stage at temperature T is the reciprocal of developmental time in days ($1/d(T=^{\circ}\text{C})$). The developmental rate data were plotted on temperature and a linear regression fit (Eq. 1).

$$\frac{1}{d} = a + bT \quad (1)$$

The lower thermal threshold for development (θ_L) was computed at $1/d=0$ as $-\frac{a}{b}$. Using θ_L , the thermal constant (K , degree days (dd)) was computed as $K=d(T-\theta_L)$ in the linear range of favorable temperatures (Campbell et al. 1974).

Effects of temperature on R_0 , r_m and fecundity

Our experimental data for R_0 , r_m and total fecundity and similar data from the literature were plotted on T . Non-linear concave polynomial functions were fit to both data sets. These functions provide estimates of the minimum, maximum and optimum temperatures for R_0 , r_m and total fecundity.

Diapause experiments

Preliminary studies on SATP larvae (Tarusikirwa et al. 2020) and pupae (Kahrer et al. 2019) demonstrated high survival at low temperatures, but the mechanism was not elucidated. In insects, cold hardening and diapause are common mechanisms to survive harsh periods and may be induced in any stage. In our study, we exposed 30 replicates of five 3rd and 4th instar larvae from the rearing colony maintained at 25 °C to one of 96 combinations of temperature \times day length \times exposure periods: T (2, 5, 10, and 15 \pm 1 °C), dl (960, 900, 840, 600, 540, and 480 min) and exposure periods E (7, 14, 28, and 42 days). Test larvae were transitioned to the experimental temperatures using the scheme illustrated in Fig. 1. At the end of each exposure period, the surviving individuals (larvae and pupae) were transitioned to non-diapause laboratory conditions of 24 \pm 2 °C, 65 \pm 5% RH and 16:08 h L:D where they were observed at 2-day interval until adult emergence. The difference between observed developmental times in dd of treated pupae ($K(T, dl, E)$) to the average time under non-diapause conditions (i.e., the thermal constant K) was used as a metric of diapause.

Statistical analyses

IBM® SPSS® v21 software (2012) was used in all analyses. After confirming normality and homoscedasticity assumptions by running Kolmogorov–Smirnov test, one-way ANOVA was used to evaluate differences between the thermal requirement based on literature data and our experiments.

Results

Effects of temperature

The data on the effects of temperature on the rate of development in our experiments and those from the literature (Barrientos et al. 1998; Krechmer and Foerster 2015; Martins et al. 2016) were analyzed separately and in combination (Fig. S1 and Table 1). Fits to the combined data were made for heuristic purposes (see discussion). The results at 6 °C had high variability and mortality, and only data in the linear range of development (10–30 °C) were used in the linear regression analyses. A data point (egg stage; 0.4, 30 °C) from Krechmer and Foerster (2015) was deleted because it is an obvious outlier (Table S1).

The slopes (b) and intercepts (a) of the two sets of data for the egg stage were not statistically different ($F_{1,16} = 2.126$, $p = 0.195$ and $F_{1,16} = 1.64$, $p = 0.241$, respectively) (Fig. S1A). The lower thermal threshold for development ($\theta_{L,egg}$) from our data is 5.70 °C, and that for the literature data is 4.28 °C (Fig. S1A and Table 1). The combined data yielded $\theta_{L,egg} = 4.94$ °C (Fig. S1B and Table 1).

For the larval data, the slopes and intercepts of the developmental rate data for the two data sets were not statistically different ($F_{1,19} = 1.242$, $p = 0.297$ and $F_{1,19} = 6.907$, $p = 0.427$, respectively) (Fig. S1C). $\theta_{L,larvae}$ from our data is 5.13 °C and 8.64 °C for the literature data (Fig. S1D and Table 1).

For the pupal data, the slopes and intercepts of the developmental rate for the two data sets were not different ($F_{1,19} = 1.849$, $p = 0.269$ and $F_{1,19} = 1.387$, $p = 0.211$, respectively) (Fig. S1E). $\theta_{L,pupae}$ was 5.31 °C for our data and 8.79 °C for the literature data (Fig. S1E and Table 1), while $\theta_{L,pupae}$ for the combined data was 7.59 °C (Fig. S1F and Table 1).

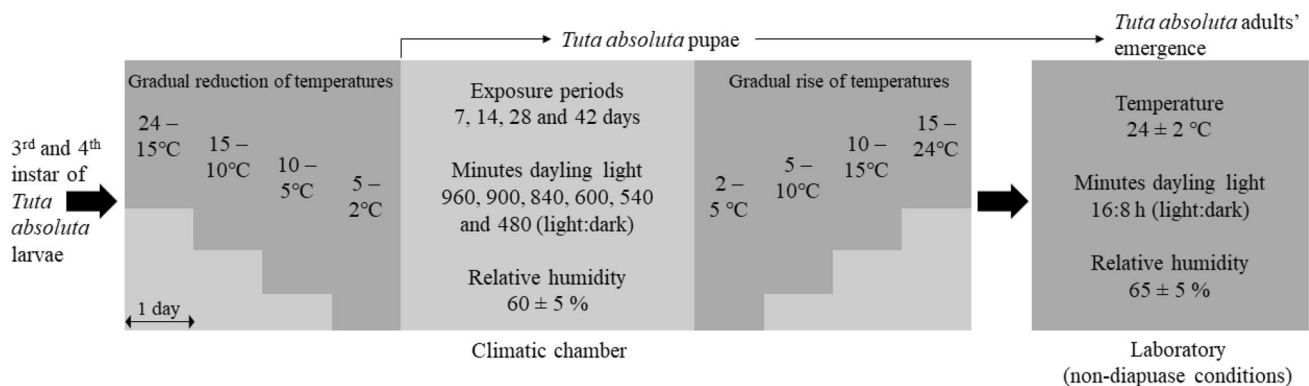


Fig. 1 Schematic diagram for the stepwise transition of temperatures in the diapause experiment for *Tuta absoluta*

The slopes and intercepts from egg eclosion to adult emergence (subscript E-A) were not statistically different ($F_{1,19}=1.084$, $p=0.328$ and $F_{1,19}=0.630$, $p=0.448$, respectively) (Fig. 2). $\theta_{L,E-A}$ from our data was 5.80°C ($R^2=0.992$), while the literature data yielded 8.28°C ($R^2=0.986$ [Fig. 2 and Table 1]). The combined data gave $\theta_{L,E-A}=7.38^\circ\text{C}$ (Fig. 2 and Table 1).

The developmental times for all life stages on temperature are summarized in Table 2. No eggs hatched at 6°C , and no development of any stage occurred at 36°C . Developmental times in days for all life stages decreased with increasing temperature, but began to increase above 33°C . Similarly, the longevity of adults in days decreased with increasing temperatures, with a sharp decline at 33°C , with no survival at 36°C (Table S2).

The effects of temperature on life table parameters

The life table statistics are summarized in Table 3. For comparative purposes, the vital rates from the literature and our studies were also combined.

The combined data on net reproduction (R_0) data were fit with 3rd-order polynomial ($R^2=0.795$, $p=0.01$) (Fig. 3A), and our experimental data were fit with a 6th-order polynomial ($R^2=0.963$ and $p=0.003$; Fig. 3B). The combined data for r_m are right skewed and were fit with 4th-order polynomial yielding lower and upper temperature thresholds for r_m of $\theta_{L,rm}=6.65^\circ\text{C}$ and $\theta_{U,rm}=36.16^\circ\text{C}$, with a maximum at $\sim 22.5^\circ\text{C}$ ($R^2=0.764$; Fig. 3C). A 3rd-order polynomial fit to our data yielded $\theta_{L,rm}$ and $\theta_{U,rm}$ estimates of 6.49°C

and 33.82°C , respectively, with a maximum at $\sim 25^\circ\text{C}$ ($R^2=0.990$; Fig. 3D).

As expected, generation time (τ) decreased with increasing temperatures (Table 3), with the longest being 103.04 days at 10°C .

Total fecundity per female using the combined data was fit with 6th-order polynomial ($R^2=0.812$ and $p=0.001$; Fig. 3E), yielding $\theta_{L,sec}$ and $\theta_{U,sec}$ values for oviposition of 6.10°C and 34.16°C , respectively. Our data were fit with a 2nd-order concave polynomial ($R^2=0.916$ and $p=0.011$) with $\theta_{L,sec}=5.37^\circ\text{C}$ and $\theta_{U,sec}=35.69^\circ\text{C}$ (Fig. 3F).

Temperature affected the age-stage-specific survival (S_{xj}) or the probability that a newly hatched larva survives to age x and stage j . Figure S2A-F illustrates the transition between life stages showing the dispersion of developmental times of cohort members (Fig. S2A-F). The age-specific survival (l_x) curves at the six constant temperatures are illustrated in Fig. S3.

Reproductive lifespan

Data on the effects of age on daily oviposition at six constant temperatures are illustrated in Fig. 4A, B. Peak oviposition occurred on the second day with the oviposition rate declining to very low levels at 15 days. The age-specific oviposition surface as affected by temperature was fit by combining two functions (Eq. 2): an exponentially decreasing function for the effect of age at optimal $T=20.53^\circ\text{C}$ and a normalized concave scalar function ($0 \leq \phi(T) \leq 1$) in favorable range ($T_{\min}=5.37^\circ\text{C}$, $T_{\max}=35.69^\circ\text{C}$) of the data (Fig. 3F:

Fig. 2 Linear regression of the development rate of *Tuta absoluta* egg to adult period on temperatures. Our experimental data (thin solid line), literature data (dash line) and the combined data (thick solid line) were fit with linear regressions

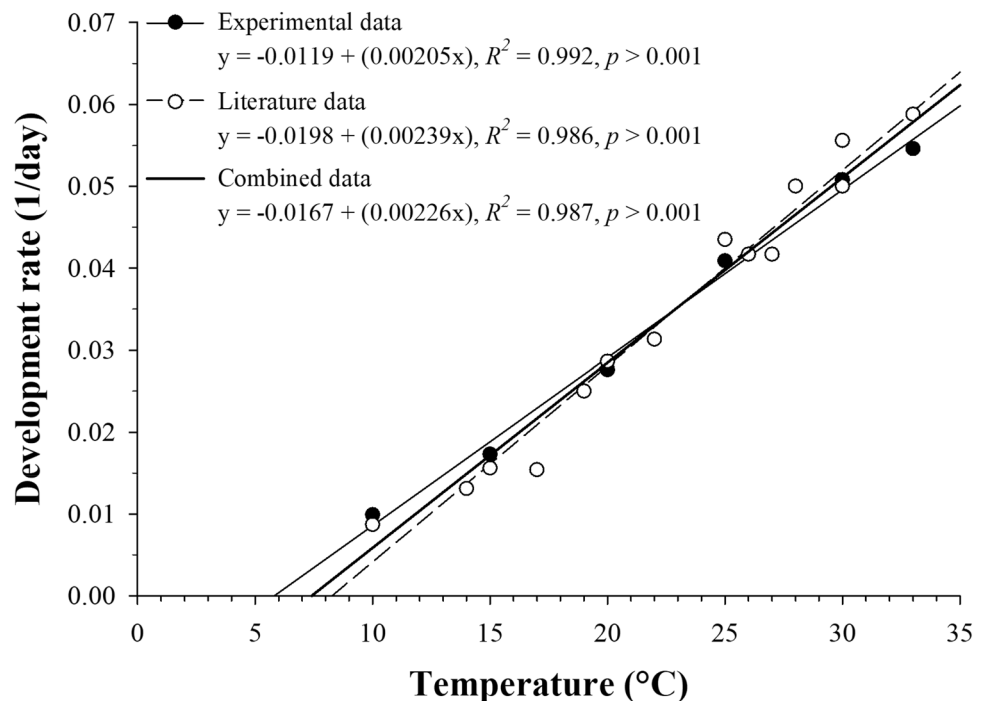


Table 1 The lower developmental threshold temperature (θ_L) and thermal constant in degree-days (K) estimated for the immature stages of *Tuta absoluta* based on our experiment data, literature data, and the combined data using the linear model

Model	Linear regression		θ_L	K	R^2	p -model
Parameters	a	b				
Life stages of <i>Tuta absoluta</i>						
eggs	Experimental data	-0.0633	0.0111	5.7027	90.0900	0.0001
	Literature data	-0.0347	0.0081	4.2839	123.4567	0.0001
	Combined data	-0.0445	0.0090	4.9444	111.1111	0.0001
	F and p -value	$F_{1,16} = 1.638$, $p = 0.2414$	$F_{1,16} = 2.120$, $p = 0.1951$			
Larvae	Experimental data	-0.0190	0.0037	5.1351	270.2703	0.0001
	Literature data	-0.0441	0.0051	8.6470	196.0784	0.0001
	Combined data	-0.0340	0.0046	7.3913	217.3913	0.0001
	F and p -value	$F_{1,19} = 6.9070$, $p = 0.4270$	$F_{1,19} = 1.2420$, $p = 0.2970$			
Pupae	Experimental data	-0.0356	0.0067	5.3134	149.2537	0.0001
	Literature data	-0.0730	0.0083	8.7951	120.4819	0.0001
	Combined data	-0.0585	0.0077	7.5974	129.8701	0.0001
	F and p -value	$F_{1,19} = 1.3870$, $p = 0.2110$	$F_{1,19} = 1.8490$, $p = 0.2690$			
Eggs-adults	Experimental data	-0.0119	0.0020	5.8048	487.8048	0.0001
	Literature data	-0.0198	0.0024	8.2845	418.4100	0.0001
	Combined data	-0.0167	0.0022	7.3893	442.4778	0.0001
	F and p -value	$F_{1,19} = 0.6300$, $p = 0.4480$	$F_{1,19} = 1.0840$, $p = 0.3280$			

Table 2 Development time (days) (mean \pm SE) of the different life stages of *Tuta absoluta* recorded at eight constant temperatures

Temperatures (°C)	Immature stages (days)			Egg to adults
	Eggs	Larvae	Pupae	
6	–	79.42 \pm 3.46 a	44.80 \pm 1.02 a	124.22 \pm 3.31 a*
10	22.77 \pm 0.62 a	48.30 \pm 0.68 b	30.44 \pm 0.93 b	119.56 \pm 2.33 b
15	9.32 \pm 0.27 b	32.16 \pm 0.65 c	16.46 \pm 0.68 c	75.18 \pm 0.93 c
20	6.27 \pm 0.20 c	19.42 \pm 0.52 d	10.78 \pm 0.49 d	48.87 \pm 1.47 d
25	4.80 \pm 0.11 d	12.30 \pm 0.46 d	7.37 \pm 0.13 d	24.47 \pm 1.10 d
30	3.70 \pm 0.15 d	12.46 \pm 0.13 d	5.55 \pm 0.12 e	21.71 \pm 1.21 de
33	3.73 \pm 0.08 d	10.10 \pm 0.32 d	5.71 \pm 0.22 e	21.43 \pm 1.48 e
36	–	–	–	–

*Egg hatch to adult emergence

Gutierrez et al. 2018). Equation 2 captures reproduction across the full range of age and temperature mapping the oviposition data in Fig. 3A.

$$\begin{aligned} \text{eggs/day/female} &= \phi(T)(ae^{(-bx)}) \\ &= (-78.66 + 16.84T - 0.41T^2)(54.753e^{(0.245 \text{ age})}) \\ \phi(T) &= 1 - \left[\frac{(T - T_{\min} - T_{\text{mid}})}{T_{\text{mid}}} \right]^2, \\ \text{with } T_{\text{mid}} - \frac{(T_{\max} - T_{\min})}{2} &= 20.53^\circ\text{C} \end{aligned} \quad (2)$$

Diapause

To determine if diapause occurs, we compared the post-treatment developmental times of individual subjected to assumed diapause inducing conditions (i.e., $K[T, dl, E]$) to the average developmental time constant ($K = 136.83dd$) of individuals under non-diapause conditions. We used the conservative $\theta_L = 7.38^\circ\text{C}$ for the egg to adult period computed from the combined data (Fig. 2 and Table 1) to compute all post-treatment developmental times of individuals in these experiments. The multiple linear regression analysis of the data for all individuals across all treatment is Eq. 3i.

$$\begin{aligned} K(T, dl, E) &= 105.4 - 5.601T + 0.0377dl + 9.619E \\ &\quad - 0.478T \times E - 0.0051dl \times E + 0.00018T \times dl \times E \end{aligned} \quad (3i)$$

$$R^2 = 0.578, df = 6013, F = 1374.17$$

All of the independent variable and interaction terms, except $T \times dl$, were significant ($15.01 < t_{\text{value}} < 23.31$, $p < 0.05$). Note that the effects of temperature are negative and that the

Table 3 Means (\pm SE) of net reproductive rate (R_0), finite rate of increase (λ), intrinsic rate of increase (r_m) and mean generation time (τ) of *Tuta absoluta* under six constant temperatures estimated by bootstrap sampling (10,000 replicates)

Temperatures (°C)	Life table parameters of <i>Tuta absoluta</i>			
	R_0	λ	r_m	τ
10	14.10 \pm 4.12 bc	1.02 \pm 3.38 e	2.56 $10^{-2} \pm 3.30 \cdot 10^{-3}$ e	103.04 \pm 1.77 a
15	25.17 \pm 5.56 ab	1.05 \pm 4.32 d	5.33 $10^{-2} \pm 4.10 \cdot 10^{-3}$ d	60.57 \pm 1.27 b
20	32.72 \pm 6.49 a	1.08 \pm 4.96 c	8.16 $10^{-2} \pm 4.58 \cdot 10^{-3}$ c	27.49 \pm 1.11 c
25	36.53 \pm 9.64 a	1.15 \pm 1.34 a	14.32 $10^{-2} \pm 1.17 \cdot 10^{-2}$ a	25.12 \pm 0.60 cd
30	11.33 \pm 2.74 c	1.10 \pm 1.24 b	9.79 $10^{-2} \pm 1.12 \cdot 10^{-2}$ b	24.80 \pm 0.90 cd
33	3.13 \pm 1.50 d	1.05 \pm 2.79 cde	5.21 $10^{-2} \pm 2.69 \cdot 10^{-2}$ cde	21.91 \pm 1.89 d

Means followed by different letters in columns indicate significant differences among treatments (paired bootstrap test, $P < 0.05$)

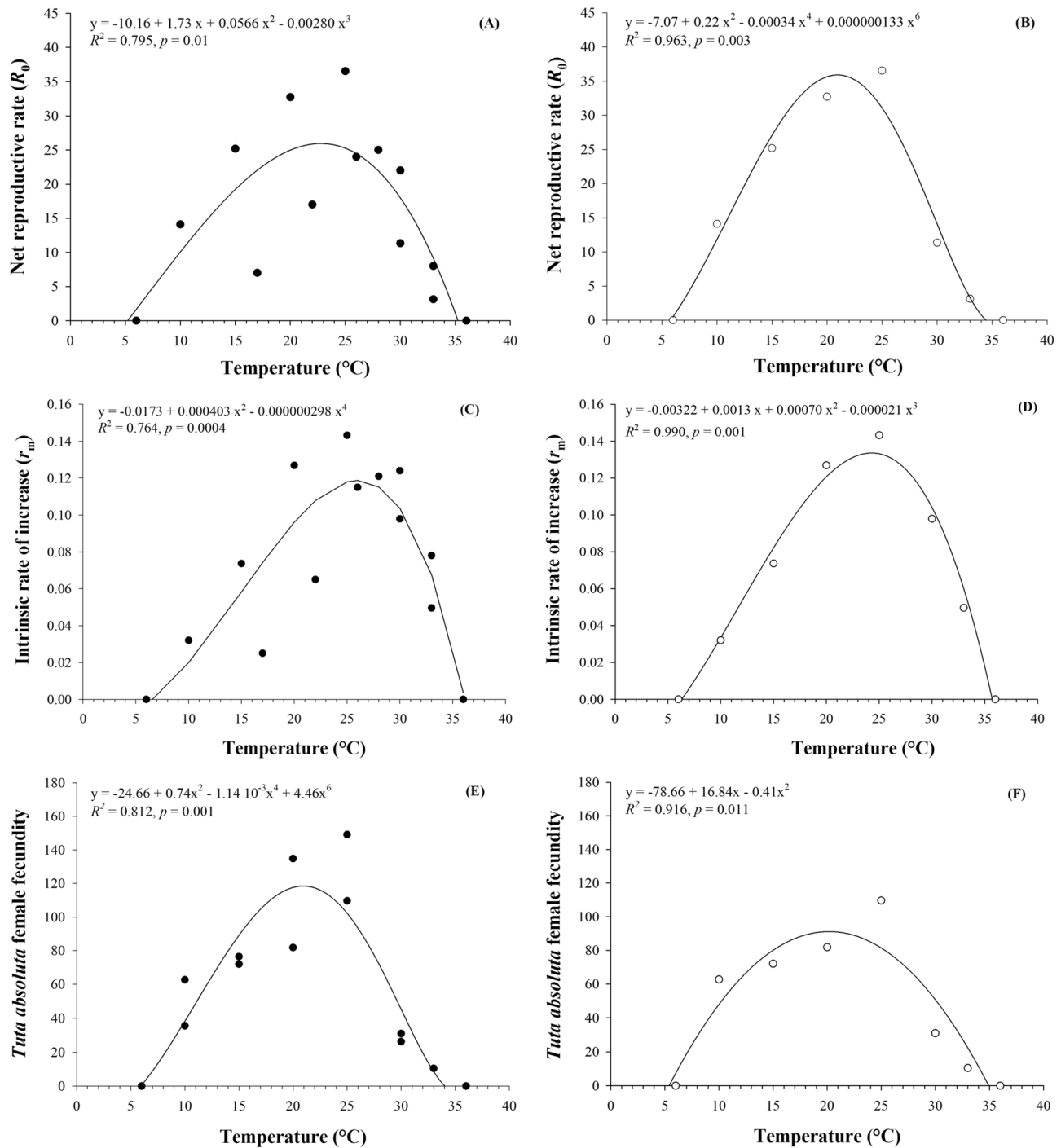


Fig. 3 Net reproductive rate (R_0), intrinsic rate of increase (r_m) and fecundity per female of *Tuta absoluta* at constant temperatures. Data from the literature and our experiments are combined in A, C, and E,

while only the experimental data are plotted in B, D, and F and are used to estimates θ_L and θ_U for each *T. absoluta* life table parameter

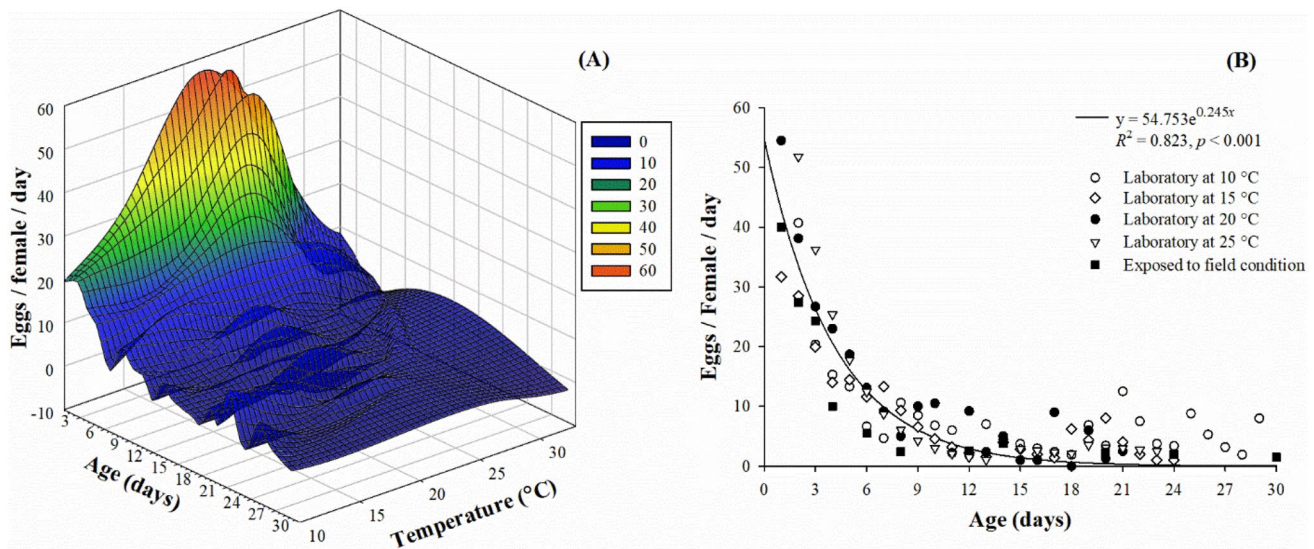


Fig. 4 Age-specific oviposition of *Tuta absoluta* females at six constant temperatures (10, 15, 20, 25, 30 and 33 °C). The data for egg/female/day are plotted as a 3-D figure on age (days) and temperature (a), while a statistical fit to all of the data eggs/female/day on age

(days) across temperatures is illustrated in (b). All females used in the experiments were derived from populations exposed to winter field condition (see text)

contribution of dl ($t_{\text{value}} = 5.01$) to R^2 is about ~0.2% estimated by removing dl from the regression. The negative effect of T in Eq. 3i is due to the fact that treatment temperatures 10 and 15 °C are above the θ_L allowing development to continue during the treatment (see above).

Removing the 10 and 15 °C treatment data, the resulting regression model is Eq. 3ii. All independent variables and interactions terms except $T \times dl \times E$ are significant ($p < 0.05$; $14.51 < t_{\text{value}} < 23.31$), with the contribution of dl to R^2 increasing to 8%.

$$K(T \leq 5^\circ\text{C}, dl, E) = -81.4 - 29.59T + 0.148dl + 15.20E - 0.0165T \times E - 1.132T \times dl + 0.0074dl \times E \quad (3ii)$$

$$R^2 = 0.684, df = 2263, F = 814.43$$

Simplifying the notation, we define $\kappa = K(T, dl, E)$. To estimate the effect of each independent variable (T, dl, E) on post-treatment developmental times (i.e., the duration of diapause), we take the partial derivative with respect to each independent variable, using the average values of the other (i.e., $T = 3.74^\circ\text{C}$, $dl = 730$ min and $E = 17.69$ days). For example, $\partial\kappa/\partial T = 29.59 - 0.165dl - 1.132 = -110.88dd$ estimates the decrease in the duration of diapause per degree increase in temperature. Similarly, $\partial\kappa/\partial dl = -0.60dd$ is the decrease per minute increase in dl , and $\partial\kappa/\partial E = 5.563dd$ is the increase per day of exposure time. By far, the most consistent response is to E ($t_{\text{value}} = 34.13$), then T ($t_{\text{value}} = 10.28$),

and dl ($t_{\text{value}} = 8.48$). The data for $K(T, E)$ are mapped on E and $T \times dl$ in Fig. 5A, B.

The mean and standard deviation of developmental times (dd) of pupae that survived to adult emergence ($K(T, dl, E)$) are summarized in Table 4 with the relevant comparisons being to the developmental times of non-treatment pupae K (i.e., $136.83dd$). The post-treatment developmental times for 7 day exposure at 2 or 5 °C are the same as K . However, the developmental time of treated pupae increases with exposure time E , with pupae from the 42 day treatments

at 2 and 5 °C requiring an average of $407.65dd \pm 125.13$ and $334.59dd \pm 82.6$, respectively, to complete development (Table 4). The results shows a clear facultative diapause in $K(T, dl, E)$ pupae with average developmental times being threefold $> K$ at 2 °C and 2.45-fold at 5 °C. The proportions of pupae satisfying the inequality $K(T, dl, E) > K$ ranged from 60 to 80% at 2 and 5 °C and exposure periods 14, 28 and 42 days (Fig. 5C). The percentage diapause in the 7 day treatments ranged from 6 to 15% at 2 and 5 °C (Fig. 5C).

The mortality of pupae at 2 °C was 90% after 42 days, but decreased with shorter exposure periods and increased temperature (Fig. 5D). The same pattern with slightly lower mortality occurred at 5 °C.

Discussion

Temperature is an important abiotic factor exerting direct and indirect effects on SATP population development, dynamics, and invasive success (Kahrer et al. 2019; Mache-kano et al. 2018; Santana et al. 2019). Knowledge of the effects of temperature on demographic parameters can help predict the establishment and relative abundance of the pest, and could underpin the development of monitoring and control strategies for integrated pest management. However, the temperature range must be fully explored in such studies and must include the entire life cycle of the insect. During the early stages of its invasion in Europe, the effects of extreme temperatures on SATP were neglected, likely because the

Table 4 Mean and standard deviation of development times of *Tuta absoluta* in $K(T \times P)$ experiments averaged across day length treatments

Temperatures (°C)	Exposure periods (days)	Observed $K(T, dl, E)$ Mean \pm SD
2	7	135.207 \pm 35.579
	14	145.569 \pm 26.486
	28	256.748 \pm 39.599
	42	407.653 \pm 125.130
5	7	134.718 \pm 25.777
	14	170.848 \pm 29.310
	28	198.986 \pm 40.256
	42	334.593 \pm 82.613

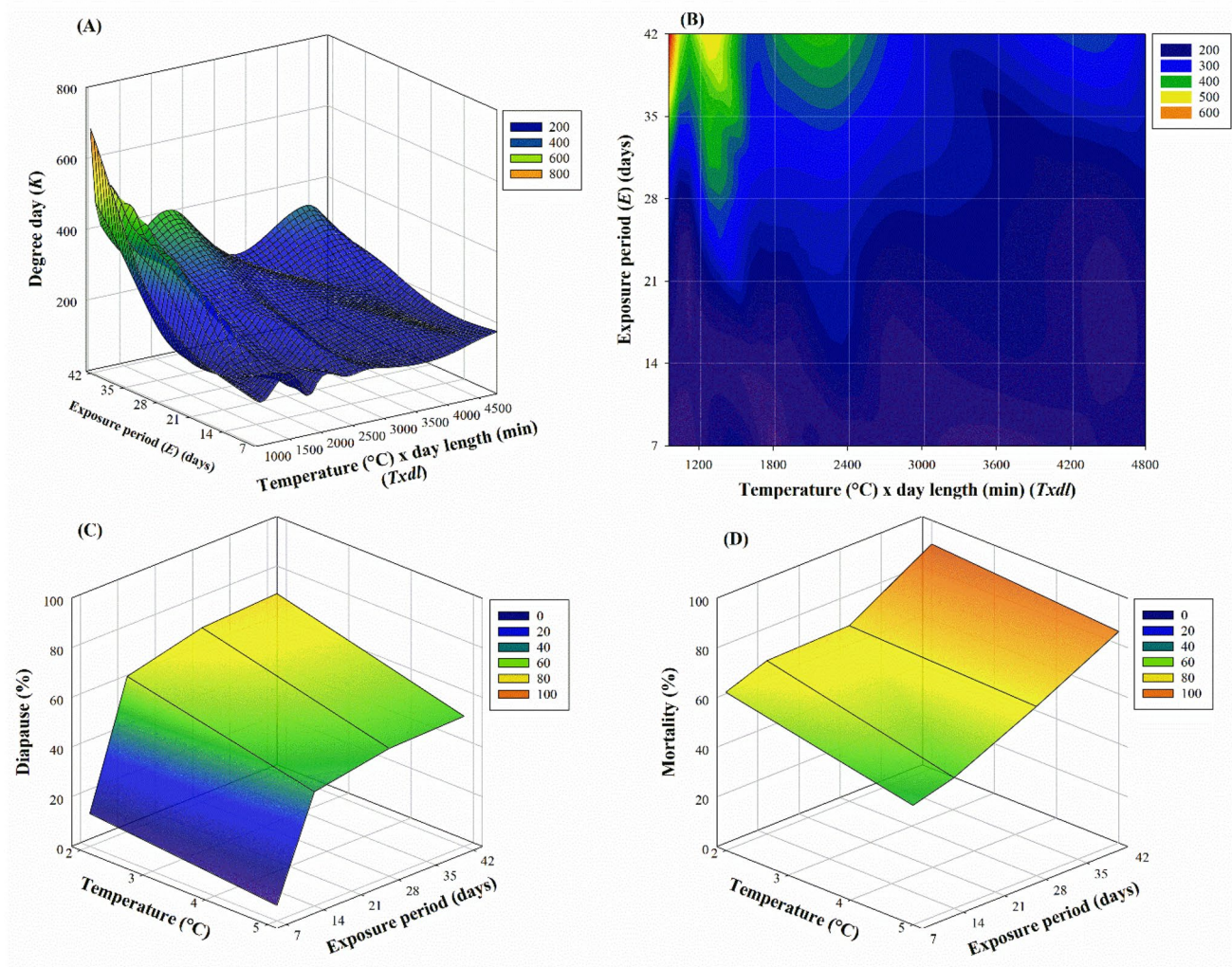


Fig. 5 Three-dimensional graphic summaries of the diapause experiment data: **(a)** a smoothed model fit of pupal developmental times (K , degree days) on the interaction of temperature (2 and 5 °C) x minutes day length ($T \times dl$) (480, 540, 600, 840, 900, 960) and on exposure

time (E , 7, 14, 28 and 42 days), **(b)** a contour map of K (sub figure **a**) across the interaction ($T \times dl$) and exposure time E , **(c)** the percentage diapause on temperatures (2 and 5 °C), and exposure times, and **(d)** the observed percentage mortality in the experimental data from C

tropical populations studied were not considered high risk for north temperate climates (Desneux et al. 2010). Early studies using South American populations are those of Barrientos et al. (1998), Krechmer and Foerster (2015), and Martins et al. 2016. The SATP's rapid spread in the colder climes of the Palearctic region was unexpected and stimulated studies to explore the thermal biology at extreme temperatures (Cuthbertson et al. 2013; Kahrer et al. 2019; Machezano et al. 2018; Van Damme et al. 2015). Our paper attempts a holistic analysis of the thermal biology of *T. absoluta* to explore some of these issues.

In the long term, natural selection on the genetic constitution of a population across generations occurs, but is slower (Nyamukondiwa et al. 2010, 2013; Sgrò et al. 2016) than required for invasion success. For successful establishment, exotic pests may have to overcome developmental obstacles in the new environment (Renault et al. 2018). Phenological variations (Briscoe et al. 2012; Chuine 2010) and phenotypic plasticity are important attributes enabling persistence in and adaptation to new, possibly harsher conditions (Manenti et al. 2017; Sgrò et al. 2016). Native environmental heterogeneity may contribute to species invasive success (Renault et al. 2018), and greater phenotypic plasticity in species coming from more heterogeneous environments may enable them to better adapt to novel environments than species from more homogenous environments (Manenti et al. 2017). The “latitudinal hypothesis” posits that developmental plasticity should increase from low to higher latitude in response to increasing thermal seasonality (Bozinovic et al. 2011; Ghalambor et al. 2007; Manenti et al. 2017).

Although SATP is thought to be from the Huancayo region in the central Andean highlands of Peru (Povolný 1994) with low variation in temperature throughout the year, the population that arrived in Europe was from central Chile, a region with broad variations in temperatures (Guillemaud et al. 2015). Our studies were conducted using a SATP population from France (45°N latitude), while the data in the literature are from Brazil (20°S and 25°S latitudes) (Krechmer and Foerster 2015; Martins et al. 2016), and from Chile (33°S) (Barrientos et al. 1998) (see weather summary in Table S3).

Thermal responses

Differences in the thermal requirement of the same species in different geographic regions are reported in the literature (e.g., *Plutella xylostella*; Lepidoptera: Yponomeutidae) (Marchioro and Foerster 2011; Shirai 2000). Linear regression analyses of the stage-specific developmental rate data from our experiments and the combined data reported in the literature from South America (Barrientos et al. 1998; Krechmer and Foerster 2015; Martins et al. 2016) show that the within stage slopes and intercepts were not significantly

different, but the estimated lower thermal thresholds for the larval and pupal stages were lower in our studies (Table 1). The differences in θ_L could be due to experimental methods (observation interval, materials), accuracy of the temperatures in the experiments, the population of SATP used, and/or to rapid adaptation after invasion in Europe (Biondi et al. 2018). For these reasons, we await confirming studies of our results on temperate populations of SATP. Hence, we used the combined data on egg to adult development from all sources to estimate the conservative lower and upper temperature thresholds of 7.38 °C and 33.82 °C, respectively.

In the range of temperatures tested (6–36 °C), only eggs did not survive at 6 °C, while no stage survived at 36 °C. Females were able to oviposit at temperatures above 6 °C, but not above 33 °C. Reproduction was highest at 20.53 °C and declined above and below this temperature. The longevity of SATP of adults was 88 days (538.6dd) in the open field at mean daily temperature of 13.5 °C, and 136 and 81 days under laboratory conditions of 10 (356.2dd) and 15 °C (617.2dd), respectively (Fig. S2A and B). Additional insights into the thermal limits of SATP were gained by fitting a nonlinear concave regression model to demographic parameters R_0 , r_m , total fecundity, age-specific fertility, and survivorship on temperature (Gutierrez 1996). The lower and upper thresholds for the demographic statistics were similar to those reported in the literature.

Diapause

Prior studies suggested that SATP has cold tolerance to otherwise lethal low temperatures (Kahrer et al. 2019; Machezano et al. 2018; Van Damme et al. 2015). We confirmed this in a field study where immature stages survived mean winter temperatures of 5.77 ± 4.29 °C, including a period when temperatures under snow dropped below 0 °C. Two types of physiological mechanisms enable insect survival during winter in the temperate zone: cold hardiness and diapause, though the relationship between them may not be separable (Denlinger 1986, 1991; Tougeron 2019). Diapause occurs during a specific stage of development, whereas cold hardiness may be expressed across a broad range of developmental stages (Denlinger 1991; Lee 1991). Diapause in insects has evolved as an adaptive strategy to survive harsh seasonal factors (temperature, moisture, food, etc.), an adaptation that is subject to both environmental influences and genetics (Tauber and Tauber 1981). Induction and maintenance of diapause under laboratory conditions have been demonstrated to vary considerably among species, geographic strains, and individuals of the same species (Fu et al. 2015; Masaki 1961). Diapause may be facultative or obligate. Facultative diapause in multivoltine species can be mediated by environmental cues inducing delayed physiological development as observed for SATP pupae.

In contrast, insects with obligate diapause enter diapause regardless of environmental cues (Danks 1987; Lees 1956; Tauber et al. 1986).

While the occurrence of diapause in SATP had not been reported for the South American strain(s), the observations of Sannino and Espinosa (2010) in Salerno, Italy, suggested the possibility of diapause in SATP. We found strong evidence for facultative diapause in SATP pupae in our experiments wherein 3rd and 4th instar larvae were exposed to 2 and 5 °C and short-day lengths for different periods. Facultative diapause in pupae was determined in treated individuals as a large increase in post-treatment developmental time of pupae after being returned to a favorable temperature. Compared to normal development, 2.45–3-fold increases in pupal developmental times occurred with low temperature and exposure time being the major contributing factors. The incidence of diapause was > 80% at 2 °C and > 60% at 5 °C.

Over the 14 years SATP has been present in Western Europe, it has gone through the process of establishment and expansion (Campos et al. 2017; Renault et al. 2018). The current level of facultative diapause in our French strain of SATP could be part of its innate plasticity, or it could have been selected during invasion of the Palearctic. In either case, it could be the springboard for greater selection for adaptation to harsher climates, enabling it to expand its range further making it even more difficult to control.

Overall, the data show that the moth has a rapid developmental time, a very short pre-oviposition period, and that it can reproduce at temperatures close to the development threshold enabling it to produce 6–9 generations per year in warmer temperate areas of the Mediterranean Basin. Furthermore, the moth is cold hardy (Kahrer et al. 2019) and, as shown here, can enter a facultative diapause as temperatures cool. These are characteristics that could enable SATP to invade large areas of the Palearctic. These insights accrued from a holistic analysis of its thermal biology.

Authors' contributions

MRC, LP, APG, AB and ND designed the research. MRC, PB and EAD led the trials. ND, AB and AA provided technical and material supports. MRC and APG analyzed the data. MRC, APG and LP wrote the manuscript. All authors read, edited and approved the manuscript.

Acknowledgements The authors wish to thank Lionel Salvy, Valérie Frandon, Anne-Violette Lavoit, Christiane Metay-Merrien, Richard Brun, Roger Boll, Sylvain Nuée, Christian Wdziekonski, Sylvain Benhamou, Anouck Lasserre, Lucie S. Monticelli, Yusha Wang, Yanyan Qu, Marianne Araújo Soares, Christine Becker, Peng Han, Timothée Fichant, Tara Malanga, Mathilda Idier, Ha Le-Thu Nguyen and Eva Thomine from INRAe for technical assistance and sharing their expertise during these studies.

Funding Project ASCII (FP7 IRSES No. 318246) for funding to ND and MRC, the University of Catania (Project 2016-18 "Emergent Pests and Pathogens and Relative Sustainable Strategies - 5A722192113) for financing to AB, the IPM Innovation Lab (USAID Cooperative Agreement No. AID-OAA-L-15-00001) for funding to ND and MRC, and the EUCLID project (H2020-SFS-2014, No. 633999) for funding to PB, EAD and ND. In kind funding accrued from the Center for Sustainable Agricultural Systems, Kensington, CA, USA. LP was supported by the MED-GOLD project that has received funding from the European Union's Horizon 2020 research and innovation programme under Grant Agreement No. 776467.

Availability of data and materials The datasets used and analyzed during the current study are available from the corresponding authors on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Consent for publication Not applicable.

Ethical approval and consent to participate Not applicable.

References






- Anastasaki E, Drizou F, Milonas PG (2018) Electrophysiological and Oviposition Responses of *Tuta absoluta* Females to Herbivore-Induced Volatiles in Tomato Plants. *J Chem Ecol* 44 (3):288–298
- Asplen MK, Anfora G, Biondi A, Choi D-S et al (2015) Invasion biology of spotted wing *Drosophila* (*Drosophila suzukii*): a global perspective and future priorities. *J Pest Sci* 88:469–494
- Bacci L, Silva EM, Martins JC, Soares MA et al (2019) Seasonal variation in natural mortality factors of *Tuta absoluta* (Lepidoptera: Gelechiidae) in open-field tomato cultivation. *J Appl Entomol* 143:21–33
- Barrientos ZR, Apablaza HJ, Norero SA, Estay PP (1998) English: threshold temperature and thermal constant for development of the South American tomato moth *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Cienc Investig Agrar* 25:133–137
- Biondi A, Desneux N, Siscaro G, Zappalà L (2012) Using organic-certified rather than synthetic pesticides may not be safer for biological control agents: selectivity and side effects of 14 pesticides on the predator *Orius laevigatus*. *Chemosphere* 87:803–812
- Biondi A, Guedes RNC, Wan F-H, Desneux N (2018) Ecology, World-wide Spread, And Management Of The Invasive South American Tomato Pinworm, *Tuta absoluta*: past, present, and future. *Annu Rev Entomol* 63:239–258
- Bozinovic F, Bastías DA, Boher F, Clavijo-Baquet S et al (2011) The mean and variance of environmental temperature interact to determine physiological tolerance and fitness. *Physiol Biochem Zool* 84:543–552
- Briere J-F, Pracros P, Le Roux A-Y, Pierre J-S (1999) A novel rate model of temperature-dependent development for arthropods. *Environ Entomol* 28:22–29
- Briscoe NJ, Porter WP, Sunnucks P, Kearney MR (2012) Stage-dependent physiological responses in a butterfly cause non-additive effects on phenology. *Oikos* 121:1464–1472
- Campbell A, Frazer BD, Gilbert N, Gutierrez AP et al (1974) Temperature requirements of some aphids and their parasites. *J Appl Ecol* 11:431–438

- Campos MR, Biondi A, Adiga A, Guedes RNC et al (2017) From the Western Palaearctic region to beyond: *Tuta absoluta* 10 years after invading Europe. *J Pest Sci* 90:787–796
- Cherif A, Attia-Barhoumi S, Mansour R, Zappalà L et al (2019) Elucidating key biological parameters of *Tuta absoluta* on different host plants and under various temperature and relative humidity regimes. *Entomol Gen* 39:1–7
- Chi H (1988) Life-table analysis incorporating both sexes and variable development rates among individuals. *Environ Entomol* 17:26–34
- Chi H (2019) TWSEX-MSChart: a computer program for the age stage, twosex life table analysis. <https://140.120.197.173/ecology/Download/Twosex-MSChart.zip>
- Chi H, Liu H (1985) Two new methods for the study of insect population ecology. *Acad Sin Inst Zool Monogr Ser Bull Inst Zool* 24:225–240
- Chi H, You M, Atlihan R, Smith CL et al (2020) Age-stage, two-sex life table: an introduction to theory, data analysis, and application. *Entomol Gen* 40:102–123
- Chaine I (2010) Why does phenology drive species distribution? *Philos T R Soc B* 365:3149–3160
- Cuthbertson GSA, Mathers JJ, Blackburn FL, Korycinska A et al (2013) Population Development of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) under simulated UK glasshouse conditions. *Insects* 4:185–197
- Danks HV (1987) Insect dormancy: an ecological perspective. Biological survey of Canada monograph series, Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Canada
- Danks HV (2007) The elements of seasonal adaptations in insects. *Can Entomol* 139:1–44
- Denlinger DL (1986) Dormancy in tropical insects. *Annu Rev Entomol* 31:239–264
- Denlinger DL (1991) Relationship between cold hardiness and diapause. In: Lee RE, Denlinger DL (eds) *Insects at low temperature*. Springer, Boston, pp 174–198. https://doi.org/10.1007/978-1-4757-0190-6_8
- Denlinger DL (2002) Regulation of diapause. *Annu Rev Entomol* 47:93–122
- Denlinger DL (2008) Why study diapause? *Entomol Res* 38:1–9
- Desneux N, Luna MG, Guillemaud T, Urbaneja A (2011) The invasive South American tomato pinworm, *Tuta absoluta*, continues to spread in Afro-Eurasia and beyond: the new threat to tomato world production. *J Pest Sci* 84:403–408
- Desneux N, Wajnberg E, Wyckhuys KAG, Burgio G et al (2010) Biological invasion of European tomato crops by *Tuta absoluta*: ecology, geographic expansion and prospects for biological control. *J Pest Sci* 83:197–215
- Efron B, Tibshirani R (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat Sci* 1:54–75
- Flitters NE, Messenger PS (1965) Effect of temperature and humidity on development and potential distribution of the Mexican fruit fly in the United States. Technical bulletin / United States Department of Agriculture. U.S. Dept. of Agriculture, Washington
- Fu S, Chen C, Xiao L, He H et al (2015) Inheritance of diapause in crosses between the northernmost and the southernmost strains of the asian corn borer *Ostrinia furnacalis*. *PloS ONE* 10:e0118186
- Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct Ecol* 21:394–407
- Gilbert N, Gutierrez AP (1973) A plant-aphid-parasite relationship. *J Anim Ecol* 42:323–340
- Goodman D (1982) Optimal life histories, optimal notation, and the value of reproductive value. *Am Nat* 119:803–823
- Guedes RNC, Picanço MC (2012) The tomato borer *Tuta absoluta* in South America: pest status, management and insecticide resistance. *EPPPO Bull* 42:211–216
- Guillemaud T, Blin A, Le Goff I, Desneux N et al (2015) The tomato borer, *Tuta absoluta*, invading the Mediterranean Basin, originates from a single introduction from Central Chile. *Sci Rep* 5:8371
- Gutierrez AP (1996) Applied population ecology: a supply-demand approach. Wiley, New York
- Gutierrez AP, Ponti L, Gilioli G, Baumgärtner J (2018) Climate warming effects on grape and grapevine moth (*Lobesia botrana*) in the Palearctic region. *Agric For Entomol* 20:255–271
- Gutierrez AP, Ponti L, Herren HR, Baumgärtner J et al (2015) Deconstructing Indian cotton: weather, yields, and suicides. *Environ Sci Eur* 27:12
- Han P, Bayram Y, Shaltiel-Harpaz L, Sohrabi F et al (2019) *Tuta absoluta* continues to disperse in Asia: damage, ongoing management and future challenges. *J Pest Sci* 92:1317–1327
- Han P, Lavoie A-V, Le Bot J, Amiens-Desneux E et al (2014) Nitrogen and water availability to tomato plants triggers bottom-up effects on the leafminer *Tuta absoluta*. *Sci Rep* 4:4455
- Han P, Zhang Y-n, Lu Z-z, Wang S et al (2018) Are we ready for the invasion of *Tuta absoluta*? Unanswered key questions for elaborating an Integrated Pest Management package in Xinjiang, China. *Entomol Gen* 38:113–125
- Itlis C, Moreau J, Pecharová K, Thiéry D et al (2020) Reproductive performance of the European grapevine moth *Lobesia botrana* (Tortricidae) is adversely affected by warming scenario. *J Pest Sci* 93:679–689
- Kahrer A, Moyses A, Hochfellner L, Tiefenbrunner W et al (2019) Modelling time-varying low-temperature-induced mortality rates for pupae of *Tuta absoluta* (Gelechiidae, Lepidoptera). *J Appl Entomol* 143:1143–1153
- Kang L, Chen B, Wei J-N, Liu T-X (2009) Roles of thermal adaptation and chemical ecology in liriomyza distribution and control. *Annu Rev Entomol* 54:127–145
- Krechemer SF, Foerster AL (2015) *Tuta absoluta* (Lepidoptera: Gelechiidae): thermal requirements and effect of temperature on development, survival, reproduction and longevity. *Eur J Entomol* 112:658–663
- Lactin DJ, Holliday NJ, Johnson DL, Craigen R (1995) Improved rate model of temperature-dependent development by arthropods. *Environ Entomol* 24:68–75
- Lawler JJ, White D, Neilson RP, Blaustein AR (2006) Predicting climate-induced range shifts: model differences and model reliability. *Glob Change Biol* 12:1568–1584
- Leather SR, Walters KFA, Bale JS (1993) The ecology of insect overwintering. Cambridge University Press, Cambridge
- Lee RE (1991) Principles of insect low temperature tolerance. In: Lee RE, Denlinger DL (eds) *Insects at low temperature*. Springer, Boston, pp 17–46. https://doi.org/10.1007/978-1-4757-0190-6_2
- Lee S, Lee Y, Lee S (2020) Population genetic structure of *Anoplophora glabripennis* in South Korea: invasive populations in the native range? *J Pest Sci* 93:1181–1196
- Lees AD (1956) The physiology and biochemistry of diapause. *Annu Rev Entomol* 1:1–16
- Logan JA, Wollkind DJ, Hoyt SC, Tanigoshi LK (1976) An analytic model for description of temperature dependent rate phenomena in arthropods I. *Environ Entomol* 5:1133–1140
- Machekano H, Mutamiswa R, Nyamukondiwa C (2018) Evidence of rapid spread and establishment of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in semi-arid Botswana. *Agric Food Secur* 7:48
- Manenti T, Sørensen JG, Loeschcke V (2017) Environmental heterogeneity does not affect levels of phenotypic plasticity in natural populations of three *Drosophila* species. *Ecol Evol* 7:2716–2724

- Mansour R, Brévault T, Chailleux A, Cherif A et al (2018) Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. *Entomol Gen* 38:83–112
- Marchioro C, Foerster L (2011) Development and survival of the diamondback moth, *Plutella xylostella* (L.) (*Lepidoptera: Yponomeutidae*) as a function of temperature: effect on the number of generations in tropical and subtropical regions. *Neotrop Entomol* 40:533–541
- Martins JC, Picanço MC, Bacci L, Guedes RNC et al (2016) Life table determination of thermal requirements of the tomato borer *Tuta absoluta*. *J Pest Sci* 89:897–908
- Masaki S (1961) Geographic variation of diapause in insects. Faculty of Agriculture, Hirosaki University: 98
- McNitt J, Chungbaek YY, Mortveit H, Marathe M et al (2019) Assessing the multi-pathway threat from an invasive agricultural pest: *Tuta absoluta* in Asia. *P R Soc B-Biol Sci* 286:1–9
- Musolin DL, Dolgovskaya MY, Protsenko VY, Karpun NN et al (2019) Photoperiodic and temperature control of nymphal growth and adult diapause induction in the invasive Caucasian population of the brown marmorated stink bug, *Halyomorpha halys*. *J Pest Sci* 92:621–631
- Nyamukondiwa C, Kleynhans E, Terblanche JS (2010) Phenotypic plasticity of thermal tolerance contributes to the invasion potential of Mediterranean fruit flies (*Ceratitis capitata*). *Ecol Entomol* 35:565–575
- Nyamukondiwa C, Weldon CW, Chown SL, le Roux PC et al (2013) Thermal biology, population fluctuations and implications of temperature extremes for the management of two globally significant insect pests. *J Insect Physiol* 59:1199–1211
- Ponti L, Gilioli G, Biondi A, Desneux N et al (2015a) Physiologically based demographic models streamline identification and collection of data in evidence-based pest risk assessment. *EPPO Bull* 45:317–322
- Ponti L, Gutierrez AP, Altieri MA (2015b) Holistic approach in invasive species research: the case of the tomato leaf miner in the Mediterranean Basin. *Agroecol Sustain Food Syst* 39:436–468
- Povolný D (1994) Gnorimoschemini of southern South America VI: identification keys, checklist of Neotropical taxa and general considerations (*Insecta, Lepidoptera, Gelechiidae*). *Steenstrupia* 20:1–42
- Rank A, Ramos RS, da Silva RS, Soares JRS et al (2020) Risk of the introduction of *Lobesia botrana* in suitable areas for *Vitis vinifera*. *J Pest Sci* 93:1167–1179
- Renault D, Laparie M, McCauley SJ, Bonte D (2018) Environmental adaptations, ecological filtering, and dispersal central to insect invasions. *Annu Rev Entomol* 63:345–368
- Requier F, Rome Q, Chiron G, Decante D et al (2019) Predation of the invasive Asian hornet affects foraging activity and survival probability of honey bees in Western Europe. *J Pest Sci* 92:567–578
- Roques A, Auger-Rozenberg M-A, Blackburn TM, Garnas J et al (2016) Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. *Biol Invasions* 18:907–920
- Sannino L, Espinosa B (2010) *Tuta absoluta*: guida alla conoscenza e recenti acquisizioni per una corretta difesa. Edizioni L'Informatore Agrario, Verona, Italy
- Santana PA, Kumar L, Da Silva RS, Picanço MC (2019) Global geographic distribution of *Tuta absoluta* as affected by climate change. *J Pest Sci* 92:1373–1385
- Sgrò CM, Terblanche JS, Hoffmann AA (2016) What can plasticity contribute to insect responses to climate change? *Annu Rev Entomol* 61:433–451
- Shirai Y (2000) Temperature tolerance of the diamondback moth, *Plutella xylostella* (*Lepidoptera: Yponomeutidae*) in tropical and temperate regions of Asia. *Bull Entomol Res* 90:357–364
- Sylla S, Brévault T, Bal AB, Chailleux A et al (2017) Rapid spread of the tomato leafminer, *Tuta absoluta* (*Lepidoptera: Gelechiidae*), an invasive pest in Sub-Saharan Africa. *Entomol Gen* 36:269–283
- Tarusikirwa VL, Mutamiswa R, English S, Chidawanyika F et al (2020) Thermal plasticity in the invasive south American tomato pinworm *Tuta absoluta* (Meyrick) (*Lepidoptera: Gelechiidae*). *J Therm Biol* 90:102598
- Tauber CA, Tauber MJ (1981) Insect seasonal cycles: genetics and evolution. *Annu Rev Ecol Syst* 12:281–308
- Tauber MJ, Tauber CA, Masaki S (1986) Seasonal adaptations of insects. Oxford University Press, New York, NY, USA
- Tonnang HEZ, Mohamed SF, Khamis F, Ekesi S (2015) Identification and risk assessment for worldwide invasion and spread of *Tuta absoluta* with a focus on Sub-Saharan Africa: implications for phytosanitary measures and management. *PlosONE* 10:e0135283
- Torres JB, Faria CA, Evangelista WS, Pratisoli D (2001) Within-plant distribution of the leaf miner *Tuta absoluta* (Meyrick) immatures in processing tomatoes, with notes on plant phenology. *Int J Pest Manag* 47:173–178
- Tougeron K (2019) Diapause research in insects: historical review and recent work perspectives. *Entomol Exp Appl* 167:27–36
- Van Damme V, Berkvens N, Moerkens R, Berckmoes E et al (2015) Overwintering potential of the invasive leafminer *Tuta absoluta* (Meyrick) (*Lepidoptera: Gelechiidae*) as a pest in greenhouse tomato production in Western Europe. *J Pest Sci* 88:533–541
- Verheggen F, Fontus RB (2019) First record of *Tuta absoluta* in Haiti. *Entomol Gen* 38:349–353

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Affiliations

Mateus Ribeiro de Campos¹  · Philippe Béarez¹ · Edwige Amiens-Desneux¹ · Luigi Ponti^{2,3}  · Andrew Paul Gutierrez^{3,4}  · Antonio Biondi⁵  · Abhijin Adiga⁶  · Nicolas Desneux¹

Antonio Biondi
antonio.biondi@unict.it

Nicolas Desneux
nicolas.desneux@univ-cotedazur.fr

¹ INRAE, CNRS, UMR ISA, University Côte d'Azur, 06000 Nice, France

² Agenzia nazionale per le nuove tecnologie, l'energia e lo sviluppo economico sostenibile (ENEA), Centro Ricerche Casaccia, Via Anguillarese 301, 00123 Roma, Italy

³ Center for the Analysis of Sustainable Agricultural Systems Global (CASAS Global), Kensington, CA 94707-1035, USA

⁴ College of Natural Resources, University of California, Berkeley, CA 94720, USA

⁵ Department of Agriculture, Food and Environment, University of Catania, Via Santa Sofia 100, Catania, Italy

⁶ University of Virginia, Charlottesville, VA 22904, USA