




# Effect of constant and fluctuating low temperature on the survival of *Tuta absoluta* pupae

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## Research Paper

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## Abstract

Temperature is among the key factors impacting the establishment and spread of invasive pests. The tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is one of the major pests attacking Solanaceae plants and is known to possess overwintering capacities. However, the cold hardiness of *T. absoluta* pupae is poorly documented. In this study, we investigated the effect of constant temperature and stepwise cooling on *T. absoluta* pupae under laboratory conditions. For this purpose, bioassays on pupal development under constant temperature (5°C) for 30, 60 and 90 days, and stepwise changes in temperature (11, 10 and 8°C; in this order every 30 days), were assessed. We found that exposure to 5°C for 30 and 60 days did not affect the post-cooling emergence time of adults compared to the control. Pupae completed their development after 60 days of cold exposure at 5°C, but more adults emerged after 30 than 60 days. Even though alive pupae were observed after 90 days of cold exposure at 5°C, no adults emerged. External colours of pupae depended on the duration of cold periods, and green pupae obtained after 30 and 60 days were found to be positively correlated with the emergence of adults. When pupae were kept at 11°C for 30 days, 47% emerged, and when the temperature was changed to 10, only 12% of pupae emerged for the period 31–60 days. However, the decrease of the temperature to 8°C yielded no emergence for the period 61–90 days. Our study provides useful information to better understand the population dynamics of overwintering *T. absoluta*, and to underpin the development of monitoring and control strategies for the pest.

## Introduction

Native to South America, the tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) is an invasive pest that has already colonised Europe, Africa and Asia (Santana *et al.*, 2019). The damage is produced when the larvae feed on the leaf mesophyll creating mines, therefore affecting the photosynthetic capacity of the plant with subsequent reduction of yield (Pereyra and Sánchez, 2006; Desneux *et al.*, 2010). *Tuta absoluta* threatens food security, incomes and livelihoods (Desneux *et al.*, 2010; Biondi *et al.*, 2018). The losses caused by *T. absoluta* and its rapid expansion favoured by trade and transport to more than 90 countries in several tomato-producing areas (open fields and greenhouses) are possible due to the high adaptability of this species to different environmental conditions (Martins *et al.*, 2016; Marchioro and Krechmer, 2023).

Environmental factors such as climatic variables directly affect the development, distribution and abundance of insects, with many species passing seasonally unfavourable periods in a state of dormancy (Wipking, 1995; Van Damme *et al.*, 2015). Among states of dormancy, diapause is a primary mechanism used by insects to adapt their life cycles to local environmental changes (Denlinger, 2002; Ahmadi *et al.*, 2018). Diapause may be quiescence, facultative or obligate, and may be induced by environmental stimuli such as temperature, photoperiod and other factors (Denlinger, 2002). Arrested development, accompanied by suppressed metabolism, can be observed in embryonic, immature and adult stages, but for some insects, the potential for cold adaptation can be restricted to a single stage (Denlinger, 2002). In *T. absoluta*, facultative diapause in pupae developing from larvae exposed to relatively low temperatures has been observed (De Campos *et al.*, 2021). Additionally, at fluctuating low temperatures commonly associated with winter conditions, *T. absoluta* surprisingly completed its development (Berckmoes *et al.*, 2012). The influence of temperature on *T. absoluta* development is not only related to the daily temperature and rate of temperature variation but also to the exposure period to temperature (De Campos *et al.*, 2021). However, the magnitude of the relationship between constant and gradual cooling temperatures, as well as the exposure period of *T. absoluta* pupae, remains poorly documented (Kahrer *et al.*, 2019). *Tuta absoluta* is cold hardy and can enter a facultative diapause during fluctuating cold temperatures (Van Damme *et al.*, 2015). An understanding of overwintering dynamics is important since the

density of the pest in the overwintering generation influences the following year's population (Wipking, 1995; Krechmer and Foerster, 2015). Our study aims to investigate how constant low temperature and stepwise decreasing temperatures affect the survival of *T. absoluta* pupae. Knowledge of the effects of temperature on overwintering pupae can help predict the relative abundance and management of the post-winter population of *T. absoluta*.

## Materials and methods

### Host plant, *T. absoluta* rearing and choice of temperatures

Tomato plants (cv. Marmande) produced in a growth chamber at  $26 \pm 2^\circ\text{C}$ ,  $70 \pm 10\%$  RH were used in these experiments. Seeds were grown individually in plastic pots (4 cm diameter) containing soil substrate (mixture of 1 with 10% TerrAktiv® + 25% GreenFibre® Klasmann-Deilmann) and sand (1:1). After 3 weeks, seedlings were individually transplanted into plastic pots (10 cm diameter) and plants were watered three times weekly with no supply of fertilisers or chemical insecticides. Plants were used in experiments at 4 weeks post-transplanting.

Colonies of *T. absoluta* were established from plant material infested with larvae collected from greenhouses at the research and application field of the Faculty of Agriculture, University of Çukurova, Adana, Turkey ( $37^\circ 01' 47.9''\text{N}$ ,  $35^\circ 21' 40.9''\text{E}$ ). Infested plant materials were kept in Plexiglas cages, and larvae were supplied healthy potted tomato plants ( $\geq 4$  weeks old) until pupation and adult emergence. With an aspirator, emerged moths were transferred to a new Plexiglas cage and honey-drops were provided as food on the top of the cage, as well as healthy potted tomato plants ( $\geq 4$  weeks old) for oviposition. After 72 h, infested plants were removed to start a new colony. Colonies had been reared for nearly 10 generations and new insects were collected from greenhouses at the research and application field regularly, and mixed with the colonies to keep genetic variability. *Tuta absoluta* rearing was carried out at  $25 \pm 1^\circ\text{C}$ ,  $80 \pm 10\%$  RH and a 16:8 L:D photoperiod. The selected temperatures of  $5^\circ\text{C}$  (for constant cold exposure), and 11, 10 and  $8^\circ\text{C}$  (for stepwise cooling), represent the range in previous studies (Van Damme *et al.*, 2015; Krechmer and Foerster, 2015).

### Effect of constant low temperature on survival of *T. absoluta* pupae

This experiment aimed to assess the effects of constant cold temperature and different exposure periods on the survival and pupal colour of *T. absoluta* pupae. One-day-old pupae were used in this experiment. To obtain the pupae, a potted tomato plant was exposed to >200 adults (ratio of 1:1, male:female) in cages ( $55 \times 75 \times 80$  cm), where moths were allowed to lay eggs for 12 h. Thereafter, the infested plant was removed and placed in an empty cage ( $55 \times 75 \times 80$  cm) for larval development. Fresh potted tomatoes were introduced and daily observations were made until the fourth instar larvae started pupating. Ten pupae (<24 h after pupation) were placed in a Petri dish (3.5 cm diameter) containing 12 g of sterile soil and settled in a controlled environmental chamber (NÜVE®TK120, Ankara, Turkey) at  $5^\circ\text{C}$  with  $65 \pm 5\%$  RH and 16:8 (L:D) photoperiod conditions for each exposure period of 30, 60 and 90 days. The experiment was replicated eight times ( $n = 80$  pupae) per treatment. At the end of each storage period, pupae that were considered alive were transferred to a

new controlled environmental chamber (NÜVE®TK120, Ankara, Turkey) at  $25 \pm 2^\circ\text{C}$  with  $70 \pm 5\%$  RH for emergence evaluation. Alive pupae were identified by subjecting pupae to meticulous observations under a Zoom Stereo Microscope (Nikon SMZ 745T). Pupae were considered alive when they moved and squirmed, and dead when they were dry, hard and very dark. Moreover, pupae colours green, brown and dark were identified and scored. Thereafter, adult emergence was recorded daily. In addition, the pupae emergence period, emerged adults with wing malformation, adults whose emergence was incomplete and non-emerged pupae were scored. For the control treatment, the same number of pupae obtained from the *T. absoluta* rearing cages, prepared as described above, were directly transferred to standard rearing conditions ( $25 \pm 2^\circ\text{C}$  with  $70 \pm 5\%$  RH) and evaluated following the same procedure.

### Effect of stepwise cooling on survival of *T. absoluta* pupae

This experiment aimed to understand how stepwise cooling affects the survival of *T. absoluta* pupae. Temperatures of 11, 10 and  $8^\circ\text{C}$ , all with  $65 \pm 5\%$  RH and 16:08 h L:D, were used. All experiments were conducted in the same controlled environmental chamber as described above. Ten 1-day-old pupae placed in a Petri dish as described above were first subjected to  $11^\circ\text{C}$  for 30 days, then to  $10^\circ\text{C}$  for 30 days and finally to  $8^\circ\text{C}$  for 30 days. Changes from one condition to another were made by adjusting the chamber temperature without removing the pupae. Observations were made every other day to record the number of adults that emerged. At the end of the last storage period, pupae were transferred to warm conditions as described above for emergence evaluation. This assay was replicated 34 times ( $n = 340$  pupae).

### Data analysis

After confirming normality and variance homogeneity of the data with the Shapiro–Wilk and Levene's tests, respectively, one-way ANOVAs were run to assess the effect of constant temperature on post-cooling emergence days, pupal colours, the number of alive pupae and the number of adults emerged. When a significant difference was observed ( $P < 0.05$ ), the Tukey test ( $P < 0.05$ ) was used for means separation. The correlation between pupae colours and adult emergence was estimated using Pearson's correlation coefficient. A non-parametric Kruskal–Wallis test was performed to assess the effect of temperature fluctuation on the number of adults that emerged. Multiple comparisons using the function `kruskalrnc` with the package `pgirmess` (Giraudoux, 2017) were run to identify the difference between groups. All analyses were performed using R.3.5.2 software (R Core Team, 2017).

## Results

### Effect of constant low temperature ( $5^\circ\text{C}$ ) on survival and morphology of *T. absoluta* pupae

Exposure to  $5^\circ\text{C}$  for 30 and 60 days did not affect the post-treatment pupal developmental period compared to the control (table 1). However, exposure to  $5^\circ\text{C}$  significantly affected the number of alive pupae, the number of emerged and non-emerged adults and the number of interrupted emergences (table 1). The number of alive pupae after 30 days of exposure at  $5^\circ\text{C}$  was higher than it was after 60 and 90 days ( $F = 57.64$ ,  $df = 2$ ,  $P < 0.001$ ).

**Table 1.** Effect of chilling on *Tuta absoluta* pupae stored at 5°C

	Pupal developmental time	Alive pupae	Emerged adults	Adult with wings malformation	Emergence interrupted	Non-emerged pupae	F	df	P
Control	6.5 ± 1.87 a	–	9.12 ± 0.39 aA	0.00 ± 0.00 bB	0.50 ± 0.26 bB	0.87 ± 0.39 cB	194.71	3	<0.001
30 days	7.95 ± 2.10 a	9.0 ± 1.77 aA	4.50 ± 1.60 bB	0.75 ± 0.31 aA	3.37 ± 0.49 aA	2.12 ± 0.54 cC	36.45	4	<0.001
60 days	6.28 ± 4.46 a	6.5 ± 2.0 bA	0.75 ± 0.31 cC	0.37 ± 0.26 abAB	3.5 ± 0.70 aA	5.75 ± 0.86 bA	20.50	4	<0.001
90 days	–	0.62 ± 0.74 cB	0.00 ± 0.00 cC	0.00 ± 0.00 bB	0.00 ± 0.00 bB	10.0 ± 0.00 aA	1405.6	4	<0.001
F	2.92	57.64	120.89	3.08	16.75	56.01	–	–	–
df	2	2	3	3	3	3	–	–	–
P	0.061	< 0.001	< 0.001	0.043	< 0.001	< 0.001	–	–	–

Means ± SE in a column (small letter) and a row (capital letter) followed by different letters are significantly different (ANOVA,  $P < 0.05$  followed by Tukey multiple comparison test).

Ninety days of exposure yielded the lowest number of alive pupae (table 1). The number of emerged adults obtained after pupae were exposed to 5°C for 30 days was higher than after 60 days, but both were lower compared to the control. Although alive pupae were recorded, no adult emergence was observed at 90 days of exposure to 5°C. Interestingly, no difference was noted in non-emerged pupae between pupae cooled for 30 days and the control ( $F = 3.39$ ,  $df = 1$ ,  $P = 0.086$ ). Interrupted emergence at both the 30- and 60-day exposure periods was significantly higher compared to the control ( $F = 10.54$ ,  $df = 2$ ,  $P < 0.001$ ).

Additionally, alive pupae, emerged adults, adults with malformed wings, incomplete emergence and non-emerged pupae were strongly affected by exposure periods (table 1). At 30 days, half of the alive pupae emerged. However, at 60 days, the number of alive pupae that emerged was reduced by eight compared to 30 days (table 1). Cooling at 5°C for 30 days yielded the highest number of adults with wing deformities compared to the control and other treatments. Moreover, at 60 days, the number of non-emerged adults ( $F = 29.78$ ,  $df = 1$ ,  $P < 0.001$ ), as well as interrupted emergence ( $F = 12.64$ ,  $df = 1$ ,  $P = 0.003$ ), was significantly higher than the number of emerged adults (table 1).

Three external colours of pupae were observed; green, brown and dark. The external colour of pupae changed depending on exposure periods (green:  $F = 12.679$ ,  $df = 2$ ,  $P = 0.000$ , brown:  $F = 0.702$ ,  $df = 2$ ,  $P = 0.507$  and dark:  $F = 15.824$ ,  $df = 2$ ,  $P = 0.000$ ; fig. 1). The number of green pupae obtained at 30 days was higher than those recorded for the 60- and 90-day cold exposure. Ninety days at 5°C exhibited the highest number of dark pupae compared to the other shorter periods. However, no difference was observed in the number of brown pupae between the exposure periods (fig. 1).

#### Correlation between pupae external colour and the emergence of adults

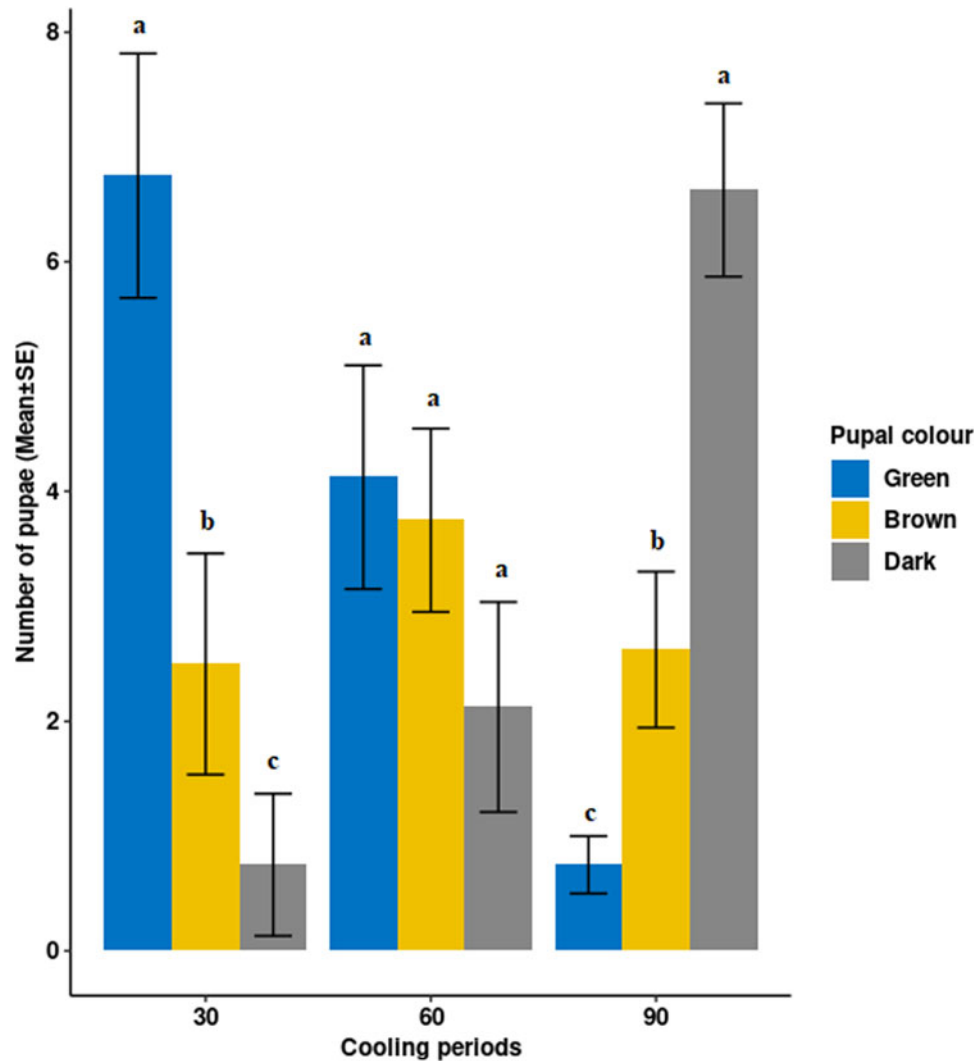
A significant correlation was observed between the number of alive pupae and green pupae ( $r = 0.83$ ,  $df = 22$ ,  $P < 0.0001$ ) and between the number of alive pupae and brown pupae ( $r = 0.44$ ,  $df = 22$ ,  $P = 0.03$ ). In contrast, no significant correlation between the number of alive pupae and dark pupae was found ( $r = 0.13$ ,  $df = 22$ ,  $P = 0.52$ ). The number of green pupae was significantly correlated with the emergence of adults ( $r = 0.69$ ,  $df = 22$ ,  $P = 0.0001$ ), whereas no significant correlation was observed between the number of brown pupae ( $r = 0.16$ ,  $df = 22$ ,  $P = 0.44$ ) or dark pupae ( $r = 0.19$ ,  $df = 22$ ,  $P = 0.36$ ) and the emergence of adults.

#### Effect of stepwise decrease of temperature on survival of *T. absoluta* pupae

Temperature decrease significantly affected the number of emerged adults ( $\chi^2 = 78.03$ ,  $df = 2$ ,  $P < 0.001$ ). The emergence rate (47%) was significantly higher during the first 30 days at 11°C than during the second at 10°C (12%) (fig. 2). When temperature decreased to 8°C at day 60, no pupae emerged until 90 days (fig. 2). First emergence was observed after 10 days exposure to 11°C and a peak of emergence was observed at days 22 and 26 followed by a decrease at 30 days (fig. 3). When the temperature was changed to 10°C, a new peak of emergence was observed at 32 and 36 days, followed by a decrease with no new emergence after day 44 and after the decrease of the temperature to 8°C for the period 61–90 days (fig. 3).

#### Discussion

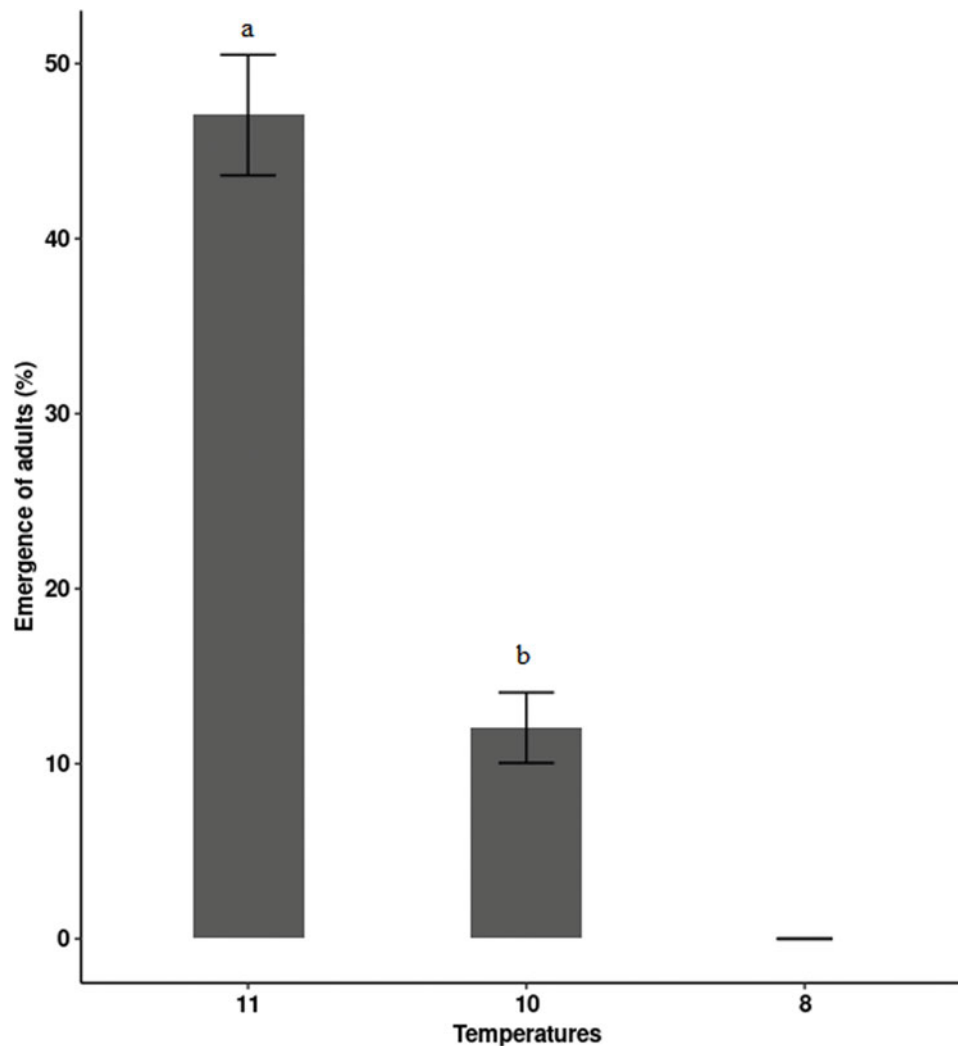
Temperature is an important abiotic factor exerting direct and indirect effects on *T. absoluta* population development, dynamics and invasion potential (Van Damme *et al.*, 2015; Kahrer *et al.*, 2019). We found that exposure to 5°C for 30 days, and also when extended to 60 days, did not affect the post-exposure emergence time of *T. absoluta* pupae compared to the control. This result indicates that pupae can sustain cold exposure without severely getting damaged and maintain their emergence period for up to 60 days. Bale and Hayward (2010) reported that when insects are subjected to low temperatures, they can reduce energy costs to retain the nutrient stock necessary for post-exposure processes; this is likely the case for *T. absoluta* pupae. In addition, the similar pupal emergence duration obtained at extended cold exposure periods (30 vs. 60 days) compared to the control, was probably due to the transfer of chilled pupae from cold conditions to normal conditions. However, after transferring 90 days pupae cooled at 5°C to normal rearing conditions, pupal emergence was hampered. This result shows that the cold tolerance mechanisms are adapted to up to 60 days before cold stress/fitness effects begin to accumulate. This would suggest that it is the cold regimed causing this effect. Thus, we considered that the similar emergence period was strongly related to the transfer of cooled pupae into normal temperature rather than cold regimes. Our findings confirmed, as reported by Van Damme *et al.* (2015) and Kahrer *et al.* (2019), that *T. absoluta* possesses cold tolerance and physiological mechanisms that enable its survival during winter (De Campos *et al.*, 2021).



**Figure 1.** State of *Tuta absoluta* pupae colours after cold exposure at 5°C. Different letters above bars show significant differences between pupal colorations (ANOVA followed by a Tukey test,  $P < 0.05$ ).

Cold conditions are known to have severe negative effects and disadvantages on the biological quality of some insect pupae (Dong *et al.*, 2013; Ahmadi *et al.*, 2018; Kahrer *et al.*, 2019). Subjecting pupae to cold conditions can result in cold stress and excessive consumption of energy reserves, thereby influencing their emergence (Shimoda and Kiuchi, 1997; Xiao *et al.*, 2013; Montini *et al.*, 2021). We found that at constant low temperatures, an extension of the storage period resulted in a decrease in the number of alive pupae and the emergence of *T. absoluta* adults. According to Van Damme *et al.* (2015), *T. absoluta* pupae that developed at 23°C and transferred to 5°C yielded viable adults, but adult mortality increased after 2 weeks of exposure. Moreover, no development takes place for larvae, pupae and adults of *T. absoluta* below 7°C (Cuthbertson *et al.*, 2013). Shimoda and Kiuchi (1997) discovered that up to 50 days, cooling was not deleterious to *Agrius convolvuli* L. (Lepidoptera: Sphingidae) pupae, while above 50 days, cooling hampered the initiation of adult emergence. Similarly, subjecting the pupae of *Pieris melete* Schrank (Lepidoptera: Pieridae) to cold conditions for 50–60 days still allowed for adult eclosion (Xiao *et al.*, 2013). Furthermore, successful emergence after cold exposure

might not guarantee the adult quality since cooling could have detrimental effects on pupae and therefore affect their survival (Özder, 2010; Chen *et al.*, 2019). These effects can differ in severity, from causing death before emergence to malformation of emerged adults (Bayram *et al.*, 2005; Chen *et al.*, 2008; Lü *et al.*, 2019). Our results show that exposure at 5°C for 30 days resulted in a higher number of adults with malformed wings (i.e. adults exhibited poor ability to fly) compared to the control. In addition, failed emergence (i.e. adults that died during emergence) after exposure to 5°C for 30 and 60 days was sevenfold higher than in the control. These results indicate that when lower pupal survival is observed, so too is the occurrence and severity of adverse effects during post-cooling development. Similarly, Turnock *et al.* (1983) reported that exposure of *Mamestra configurata* Walker (Lepidoptera: Noctuidae) pupae to continuous or interrupted cold conditions increased the number of adults with deformities and un-emerged pupae. Moreover, Martins *et al.* (2016) found that the mortality risk of *T. absoluta* pupae increased at temperatures below 22°C. Likewise, the development time of *T. absoluta* pupae was fourfold higher at a low temperature (10°C) compared to the normal regime (25°C)



**Figure 2.** Effect of gradual cooling on adult emergence of *Tuta absoluta*. Different letters above bars show significant differences between adult emergence (Kruskal–Wallis test followed by non-parametric multiple comparisons using the function `kruskalrmc`,  $P < 0.05$ ).

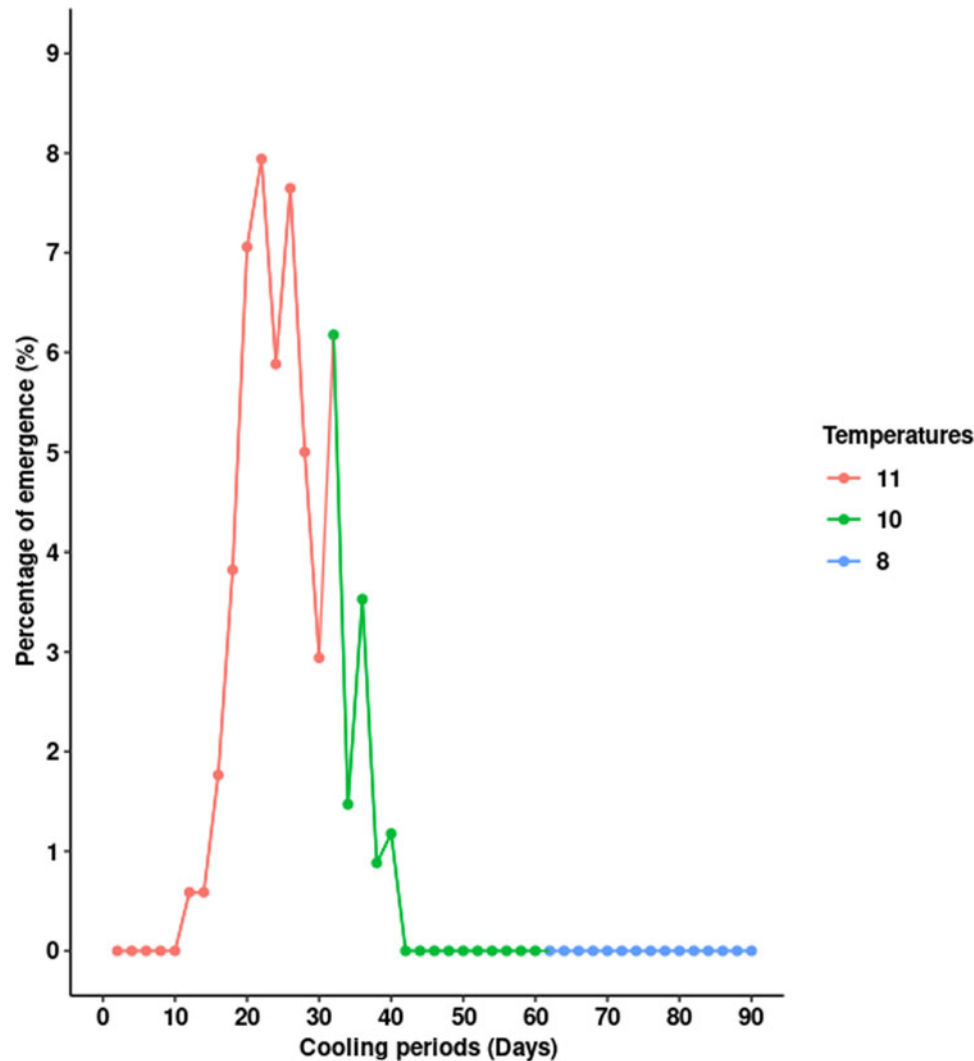
(Krechemer and Foerster, 2015). Contrary to *M. configurata*, which exhibited similar responses at low temperatures regardless of the exposure period, we assume that the effect of cold exposure on *T. absoluta* pupae was strongly exposure time-dependent.

Cooling at a constant temperature of 5°C affected the pupae colouration and post-cooling pupae exhibited three external colours; green, brown and dark. A positive correlation was identified between green pupae and emerged adults when the pupae were cooled at 30 and 60 days. Islam *et al.* (2019) reported that *Papilio demoleus* L. (Lepidoptera: Papilionidae) larvae maintained in cold conditions have more brown pupae and fewer green pupae compared to those maintained under warmer conditions. Our findings show that *T. absoluta* pupae may retain their green colouration to pass cold conditions and maximise the safety of adult emergence. Colouration affects the absorption of radiant energy, and colour variation in response to temperature may be an ectothermic adaptation to suboptimal thermal conditions (Danks, 2004; Bale and Hayward, 2010). Yamamoto *et al.* (2011) pointed out that diapaused pupae of *Byasa alcinous* (Klug) (Lepidoptera: Papilionidae) in cold conditions showed dark-brown pupal colouration while yellow colouration was induced by higher temperature and humidity conditions. Moreover, *Papilio xuthus*

L. (Lepidoptera; Papilionidae) diapaused pupae exhibit orange colouration under 25°C (Yamanaka *et al.*, 2004). Since pupal colour changes can be used as an indicator of diapause entry in *Chouioia cunea* (Yang) (Hymenoptera: Eulophidae) (Zhao *et al.*, 2014), it could also be a guide for the assessment of the diapause of *T. absoluta* pupae. The green colour maintained by pupae during cold exposure could be a cold-adaptive mechanism that enables the emergence of adult *T. absoluta*.

Fluctuating temperatures are known to have a stimulating effect on the growth and development of insects compared to constant temperatures and are a better reflection of natural conditions (Colinet *et al.*, 2015). Insects can respond to these fluctuations in ways ranging from hardening responses to evolutionary responses over geological time (Ragland and Kingsolver, 2008). We found that 11°C was not injurious and led to an acceleration of adult emergence, but a change to 10°C drastically reduced the emergence rate. We posit that the reduced mortalities at fluctuating temperatures (11 vs. 10°C) were due to the plastic response of pupae (Teets and Denlinger, 2013). Arias *et al.* (2011) stated that fluctuating temperatures that remain within the appropriate thermal range can result in accelerated development, slower development or no change in developmental rate. However, when the





**Figure 3.** Effect of temperature fluctuation on daily emergence of *Tuta absoluta*.

temperature was changed to 8°C, pupae development was hampered and no emergence was recorded for the period 61–90 days. Van Damme *et al.* (2015) inversely discovered that fluctuating temperatures during cold conditions (e.g. 5°C) and favourable conditions (e.g. 25°C) may have resulted in slight reduction in pupal mortality of *T. absoluta*. The divergence of this finding with our results might be due to the longer cooling periods in our study causing severe adverse effects to the pupae. Chown and Terblanche (2006) reported that developmental delays after exposure to fluctuating low temperatures is directly proportional to cold exposure time.

### Conclusion

This study highlighted the ability of *T. absoluta* pupae to cope with low temperatures during extended exposure periods. However, when the period was prolonged beyond 60 days, the development of pupae was hampered. Understanding *T. absoluta* pupae's overwintering capacity is essential for developing management tactics and preventing the outbreak of adults that emerge from the overwintering pupae. *Tuta absoluta* is a multivoltine insect, and a survival of 10% of the hibernating population may be sufficient for a *T. absoluta* population outbreak in the next

growing season (Van Damme *et al.*, 2015). It is important to strengthen sanitation, suitable cultivation practices and pheromones as preventive measures after a cold season.

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**Competing interests.** None.

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