INNSPUB

International Journal of Biosciences | IJB |
ISSN: 2220-6655 (Print); 2222-5234 (Online)
Website: https://www.innspub.net
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Vol. 28, Issue: 4, p. 33-40, 2026

RESEARCH PAPER

OPEN ACCESS

Effect of temperature on the development of immature stages of *Zeugodacus cucurbitae* (Diptera: Tephritidae), Coquillett, 1899, A major watermelon pest in Senegal

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Key words: *Zeugodacus cucurbitae*, Temperature, Development duration

Received: March 19, 2026 **Accepted:** April 02, 2026 **Published:** April 07, 2026

DOI: https://dx.doi.org/10.12692/ijb/28.4.33-40

ABSTRACT

Global warming strongly influences the development of *Zeugodacus cucurbitae*, a major pest of cucurbit crops; however, the effects of certain intermediate and high temperatures, as well as natural conditions particularly on watermelon remain insufficiently documented. The present study assessed the effect of a thermal gradient, including ambient temperature and constant temperatures of 25, 27, 30, and 33°C, on the development of the immature stages (egg-larva-pupa) of *Z. cucurbitae*. The results indicate that preimaginal development time exhibits a non-linear thermal response. The duration of the pupal stage decreases with increasing temperature, whereas pupal survival and total developmental time follow a unimodal pattern, characterized by accelerated development up to a thermal optimum (27°C), beyond which biological performance declines and variability increases. These findings confirm the existence of an optimal thermal window (25-27°C) for the development of *Z. cucurbitae* and reveal stage-specific thermal plasticity. This sensitivity to temperature fluctuations has important implication for phenological modeling, population dynamics forecasting, and the adaptation of integrated pest management strategies under climate change scenarios.

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INTRODUCTION

Climate warming is now an unequivocal scientific reality. According to Legg (2021), the global mean temperature has increased by approximately 1.1°C relative to pre-industrial levels, primarily due to anthropogenic activities, with a marked intensification of heatwaves and thermal extremes. Recent years rank among the warmest ever recorded, reflecting a persistent upward temperature trend (WMO, 2026). Beyond physical alterations, these changes directly affect biological systems by modifying the distribution, phenology, physiology, and population dynamics of living organisms (Trisos *et al.*, 2022). Temperature is a fundamental abiotic factor governing the distribution and functioning of organisms within ecosystems (Odum, 1971; Ricklefs, 2008). Teder *et al.* (2022) reported that it strongly influences the growth and development of ectothermic animals. Insects are typical ectotherms, characterized by high taxonomic diversity, large population sizes, and rapid reproductive rates (Chapman, 1998; Grimaldi and Engel, 2005). Their small body size, thin cuticle, rapid heat exchange with the surrounding environment, and limited capacity to maintain a stable body temperature make them particularly sensitive to environmental fluctuations (Zeng *et al.*, 2022). In agroecosystems, climate change regulates the geographic distribution of pests, the number of generations per year, survival rates, and synchronization with host plants (Britannica, 2026). *Zeugodacus cucurbitae* (Coquillett, 1899) (Diptera : Tephritidae), commonly known as the melon fly, is a major pest of tropical and subtropical cucurbit crops, causing substantial agricultural losses when populations reach high densities (Dhillon *et al.*, 2005; Meyer *et al.*, 2015; Zeng *et al.*, 2022). Like other poikilothermic insects, its development is strongly influenced by ambient temperature, which affects both the duration of the immature stages (egg, larva, and pupa) and their survival (Vayssières *et al.*, 2008; Mkiga and Mwatawala, 2015). Although several studies (Vayssières *et al.*, 2008; Mkiga and Mwatawala, 2015; Ahn *et al.*, 2022; Zeng *et al.*, 2022) have examined the effects of temperature on the development of *Z. cucurbitae*, they rarely include watermelon-one of the fly's principal host plants-and are generally restricted to a limited range of constant temperatures (20, 25, and 30°C). Moreover, these studies predominantly focus on populations from East Africa or Asia. According to Mwatawala *et al.* (2016), watermelon is the preferred host of *Z. cucurbitae*. In addition, intermediate temperatures (27°C) and those approaching the upper thermal tolerance limit (≈33°C) remain poorly documented in the scientific literature. The effects of natural ambient conditions, incorporating daily thermal fluctuations, have also not been directly compared with controlled constant temperatures.

Therefore, evaluating the development of *Z. cucurbitae* under a thermal gradient including ambient temperature and constant temperatures of 25, 27, 30, and 33°C an approach not previously implemented in Senegal helps fill a critical knowledge gap. This framework enables a more precise determination of the thermal optimum and sublethal thresholds, improves understanding of the species' thermal plasticity, and strengthens predictive tools for population management. The objective of this study is to compare the thermal responses of the different immature stages and to identify the optimal temperature ranges for their development.

MATERIALS AND METHODS

Biological material

The biological material consisted of watermelon fruits (*Citrullus lanatus*) collected at different stages of maturity from various locations.

Field sampling

Sampling was conducted in October 2025 at the Botanical Garden (14°41'3"N and 17°27'45"W) of Cheikh Anta Diop University in Dakar and at a local market (Syndicat) located in the department of Pikine (14°45'32"N and 17°23'37"W), where watermelon (*Citrullus lanatus*) was sold. The market was selected because of its central role in fruit distribution and the high likelihood of obtaining infested fruits. Despite the relatively low diversity of cucurbit crops in the botanical garden, the presence of watermelon justified its inclusion as a sampling site.

The surrounding plant diversity may contribute to ecological stability and the maintenance of insect populations, while moderate crop management practices allow the collection of samples representative of near-natural conditions. Watermelon fruits exhibiting signs of infestation (softened areas, oviposition punctures, exudates, etc. Fig. 1) were collected at each site, either directly from cultivated plots or from the ground. Fruits obtained from the market were at an advanced stage of maturity, whereas those collected from the botanical garden were still immature. At each site, collected fruits were placed in plastic bags and transported to the laboratory for incubation.

Fig. 1. Infested watermelon (*Citrullus lanatus*) fruits collected from the sampling sites

Rearing conditions

The collected fruits were incubated following the protocol described by Mendy *et al.* (2026) under five distinct environmental conditions to assess the effects of temperature and relative humidity on the immature stages of the target species. Four experimental environments were maintained in incubators set at 70% relative humidity and constant temperatures of 25°C, 27°C, 30°C, and 33°C. The fifth environment corresponded to the ambient conditions of the Entomology and Acarology Laboratory, Department of Animal Biology, where temperature fluctuated between 26 and 32°C. Temperature and relative humidity were monitored daily using a thermo-hygrometer to ensure consistency of the experimental conditions.

Determination of the oviposition period (Days)

After newly emerged adults had survived for six days in cages containing infested fruits, fresh pieces of watermelon were introduced into each cage to provide a suitable substrate for oviposition. After 24 hours, each watermelon piece was removed and incubated in a container according to the fruit incubation protocol described above. This procedure was repeated daily.

Five days after incubation, the sand contained in each container was sieved to detect the presence of pupae. The oviposition period was determined by calculating the time interval between the day of egg deposition and the day of appearance of the corresponding pupa.

Determination of the pupal duration (Days)

The duration of the pupal stage was determined by calculating the number of days between the date of pupal collection and the date of emergence of the corresponding adult.

Determination of the life cycle duration (Egg-adult) (Days)

The duration of the life cycle was determined by calculating the number of days between egg hatching and the emergence of the corresponding adult.

Statistical analyses

Data were entered into Microsoft Excel (2016) for verification and organization. Statistical analyses were performed using R software (version 4.5.2) via the RStudio interface (version 2025.09.2). Data normality was assessed with the Shapiro Wilk test. Since development times (expressed in days) did not meet the assumptions of normality, as confirmed by the Shapiro-Wilk test, the non-parametric Kruskal-Wallis test was applied, followed by Dunn's post-hoc test with Bonferroni correction for pairwise comparisons. All tests were conducted at a significance level of 0.05. Emergence rate data were binary (mortality/emergence, coded 0/1).

These were analyzed using a generalized linear model (GLM) with a binomial distribution and a logit link function, following recommended procedures for binary and proportional data in entomology (Crawley, 2012; McCullagh, 1989e; Wang *et al.*, 2020; Costaz *et al.*, 2022; Estrada-Marroquín *et al.*, 2022). Overall significance was assessed using deviance analysis (chi-square test), and multiple comparisons with Tukey adjustment were performed using the emmeans package.

RESULTS

The following results present the development times (in days) of the immature stages of *Z. cucurbitae* measured under five thermal conditions :

1. Ambient temperature (26–32°C)
2. 25°C, 70% RH (Twenty-five70)
3. 27°C, 70% RH (Twenty-seven70)
4. 30°C, 70% RH (Thirty70)
5. 33°C, 70% RH (Thirty-three70)

Duration between egg laying and pupation

Fig. 2 shows boxplots representing the duration (in days) from egg laying to pupation. Temperature had a significant effect on the development time between egg laying and pupation. At 30°C and 70% relative humidity, the median duration was highest (≈8 days), with a wide dispersion of values ; the egg-to-pupa period was significantly longer than at other temperatures ($p < 0.05$). This condition was classified in group b, indicating a significant prolongation of pre-imaginal development at this temperature. In contrast, at 33°C and 70% relative humidity, the egg-to-pupa duration was significantly shorter, with a median lower than that observed at other temperatures and moderate variability. This condition belonged to group c, reflecting a statistically significant difference compared with all other thermal conditions. Durations observed at 25°C, 27°C, and under ambient conditions did not differ significantly from each other (group a). The high variability observed at 30°C suggests a heterogeneous individual response to this thermal condition. Overall, these results indicate that temperature strongly influences pre-imaginal development time, following a non-linear pattern characterized by relative stability at moderate temperatures (ambient, 25°C, 27°C), an extension at 30°C, and a pronounced reduction at 33°C.

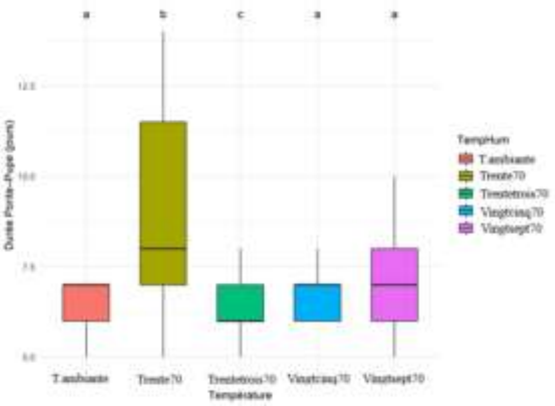

Fig. 2. Effect of temperature on the duration from egg laying to pupation of *Z. cucurbitae*

Letters (a, b, c) above the boxes indicate statistical groups based on a Dunn post-hoc test, where different letters denote a significant difference ($p < 0.05$) and identical letters indicate no significant difference.

Pupal-adult duration

Temperature variations had a statistically significant effect on the duration of development from the pupal stage to adult emergence (Fig. 3). At 25°C and 70% relative humidity, the pupal–adult duration was significantly longer, with a high median and marked variability.

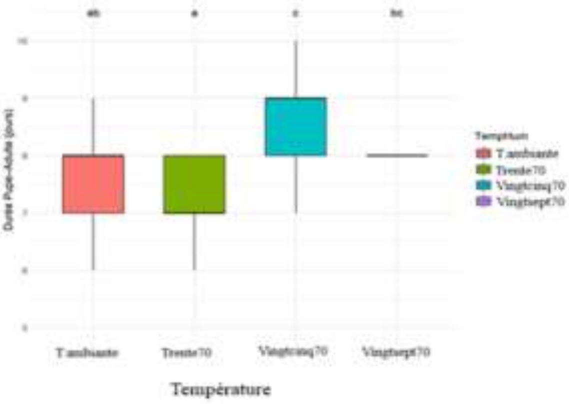

Fig. 3. Effect of temperature on the pupal–adult stage duration of *Z. cucurbitae*

This condition was classified in statistical group c, indicating a significant difference compared with all other temperatures. These results suggest a slowdown of pupal development at this temperature. At 30°C and 70% relative humidity, the pupal stage was the shortest, with a median lower than that of other temperatures and relatively low variability.

This condition was classified in group a, reflecting accelerated pupal development at this temperature. Under ambient conditions, the pupal–adult duration showed an intermediate median with moderate variability. This condition belonged to statistical group ab, indicating no significant difference from 27°C and 30°C, but a partial difference from 25°C. At 27°C and 70% relative humidity, the median was similar to that observed under ambient conditions. The low variability observed indicates a relatively homogeneous individual response. This condition was classified in group bc, showing no significant difference from ambient conditions or 25°C, but differing from 30°C.

Pupa emergence rate

Analysis using a generalized linear model (GLM) with a binomial distribution revealed a highly significant effect of temperature on pupal emergence ($\chi^2 = 62.76$; df = 3; $p < 0.001$).

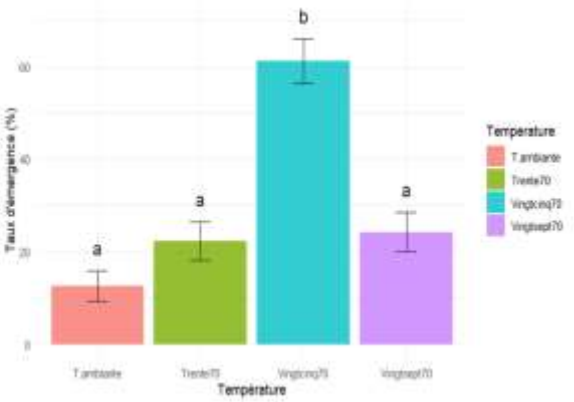

Fig. 4. Effect of temperature on the emergence rate of *Z. cucurbitae* pupae

Detailed values are presented in Fig. 4, which illustrates the distribution of the data. The emergence rate at 25°C (61.2%) was significantly higher than at ambient temperature (12.6%), 27°C (24.3%), and 30°C (22.3%) ($p < 0.0001$ for all pairwise comparisons). This difference is further confirmed by Fig. 4, which shows no overlap between the 25°C box and those of the other groups. The barplots also highlight an increasing heterogeneity in the response with rising temperature: the distribution was very narrow at 25°C (IQR = 1%), broader at 27°C (IQR = 9%), and highly dispersed at 30°C (IQR = 15%).

Overall, these results indicate that 25°C is the optimal temperature for adult emergence, while 27°C and 30°C are associated with intermediate and similar emergence rates. Ambient temperature was unfavorable for emergence.

Development time

Temperature had a significant effect on the total development time of the immature stages of *Z. cucurbitae* (Fig. 5). Treatments in the same statistical group (ambient conditions, 27°C–70% RH) exhibited a relatively short total development time with low variability, with a median of approximately 15 days. In contrast, at 30°C–70% RH, development was significantly prolonged, with a median around 19 days and a wide dispersion of values. This treatment was classified in group b and did not differ significantly from 25°C-70% RH, which had a median of about 17 days and moderate variability.

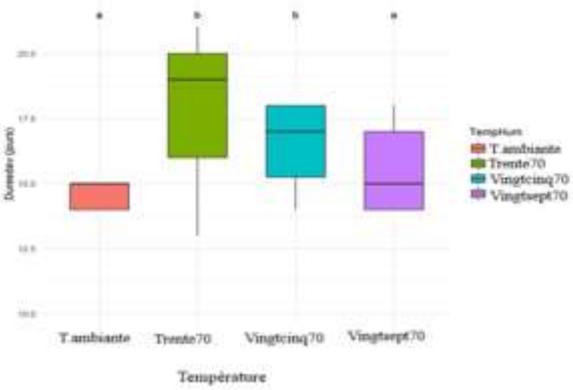

Fig. 5. Effect of temperature on the total development time of *Z. cucurbitae*

Overall, these results indicate that the development time of *Z. cucurbitae* follows a pronounced but non-linear thermal response. The shortest development times occurred under ambient conditions and at 27°C, whereas significant prolongation was observed at 25°C and, particularly, at 30°C under 70% relative humidity.

DISCUSSION

The objective of this study was to examine the effect of temperature on the development time of the immature stages of *Zeugodacus cucurbitae*. The results reveal a complex and significant thermal response, confirming the crucial role of temperature in the developmental dynamics of this species. Development time from egg laying to pupation exhibited a non-linear thermal response, whereas the pupal–adult duration decreased with increasing temperature. The total life cycle duration followed a unimodal pattern. This non-linearity in pre-imaginal development reflects the high sensitivity of the egg and larval stages to temperature variations, as these stages are characterized by distinct thermal thresholds and optima (Schoolfield *et al.*, 1981; Jaworski and Hilszczański, 2013; Mkiga and Mwatawala, 2015; Rebaudo *et al.*, 2018). According to the enzymatic model proposed by Schoolfield *et al.* (1981), the development of poikilothermic organisms is governed by temperature-dependent biochemical reactions, which accelerate up to an optimum before being inhibited by enzymatic inactivation at high temperatures.

The stability of development time observed between 25 and 27°C suggests that this temperature range provides favorable conditions for the physiological processes underlying pre-imaginal development. Temperature directly affects insect metabolic rates, leading to variations in the time required to complete development (Gillooly *et al.*, 2001). Régnière *et al.* (2012) demonstrated that, within intermediate temperature ranges, fluctuations in temperature result in only minor changes in development time, in contrast to suboptimal or extreme thermal zones. Similar findings have been reported in Tephritidae, where the development time of immature stages is minimal or relatively stable within an intermediate thermal range (Danjuma *et al.*, 2014).

Our results corroborate those of Mkiga and Mwatawala (2015), who reported that the development of the egg, larval, and pupal stages of *Z. cucurbitae* is accelerated at 25°C and 30°C compared to 20°C, with high survival rates at 25°C. Similarly, Ahn *et al.* (2022) estimated, using modeling approaches, that optimal development occurs between 24 and 26°C, with the complete development range extending up to approximately 36°C. These findings support the existence of a favorable intermediate thermal range, within which development duration remains relatively stable before physiological constraints emerge at lower or higher temperatures.

However, unlike some previous studies (Vayssières *et al.*, 2008; Mkiga and Mwatawala, 2015; Ahn *et al.*, 2022), our results did not show a reduction in development time at 30°C. This discrepancy suggests the presence of a thermal transition zone, in which further increases in temperature no longer accelerate development. According to Régnière *et al.* (2012), approaching suboptimal thermal conditions can induce physiological constraints, leading to prolonged development times. Elevated temperatures may also trigger cellular protective mechanisms, such as the induction of heat shock proteins (HSPs), and impair the efficiency of enzymatic and hormonal systems when operating outside their optimal range (Feder and Hofmann, 1999; Hofmann, 1999; Angilletta, 2009). These mechanisms entail an energetic cost that can slow growth (Feder and Hofmann, 1999; Angilletta, 2009).

Furthermore, at high temperatures, water-rich fruits such as *Citrullus lanatus* experience accelerated respiration, fermentation, and microbial spoilage (Bateman, 1972; Kader, 2002). This substrate degradation can reduce the nutritional quality available to larvae and limit their growth performance. Discrepancies with previous studies may also be explained by differences in local adaptation and phenotypic plasticity among the populations studied. Several studies have shown that ectothermic insect populations exhibit variable thermal responses depending on their geographical origin (Rodrigues and Beldade, 2020; Hafsi *et al.*, 2024).

At 33°C, although the development of immature stages was accelerated, no adult emergence was observed. This indicates that this temperature exceeds the critical thermal threshold for pupation and emergence in the Senegalese population of *Z. cucurbitae*, thus representing an upper thermal tolerance limit. This response corresponds to a supra-optimal zone, characterized by increased metabolic rates that can shorten development time but are incompatible with completion of the life cycle (Angilletta, 2009). For the pupal-adult stage, the decrease in development time with increasing temperature aligns with established principles of insect thermal biology (Gillooly *et al.*, 2001; Irlich *et al.*, 2009; Régnière *et al.*, 2012). However, despite faster development at 27–30°C, emergence rates remain markedly lower than at 25°C, indicating moderate thermal stress for the pupal stage. This observation contrasts with the results of Mkiga and Mwatawala (2015), who reported maximum survival at 30°C, a divergence likely attributable to local adaptations to thermal regimes (Neven, 2000; Kingsolver and Huey, 2008; Sinclair *et al.*, 2012).

Finally, the total duration of the development cycle exhibits a non-linear thermal response. Ambient conditions result in faster but highly variable development, likely due to daily temperature fluctuations. Temperatures of 25 and 27°C are associated with intermediate durations and low variability, indicating proximity to the physiological optimum. At 30°C, the prolongation of the cycle and increased variability reflect the onset of thermal stress. These findings are consistent with the predictions of metabolic theory (Gillooly *et al.*, 2001) and suggest that the Senegalese population of *Z. cucurbitae* is adapted to hot and variable climatic conditions, with an optimal thermal range around 25-27°C (Sinclair *et al.*, 2012).

CONCLUSION

Temperature is a key factor regulating the development of *Z. cucurbitae*, affecting the larval and pupal stages in distinct ways. The duration of development from egg laying to pupation exhibits a non-linear thermal response, whereas the pupal phase shortens as temperature increases. Overall, pupal survival and total life cycle duration follow a unimodal thermal pattern, characterized by accelerated development up to an optimal temperature, beyond which higher temperatures induce developmental slowdown and increased variability. These findings emphasize that the biological performance of *Z. cucurbitae* is maximized within a narrow thermal window, confirming the existence of a physiological optimum and highlighting the species' sensitivity to thermal fluctuations. This thermal plasticity, together with stage-specific variability in responses, has important implication for understanding population dynamics and predicting the species' spread under different climatic scenarios.

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