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Assessing the Impact of Elevated Temperature on Reproductive Success in Fall Armyworm

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Authors' contributions

This work was carried out in collaboration among all authors. Authors VME and RJS conceptualized the work. Authors RJS and VME carried out the experiments. Authors SPN and SSP helped in data analysis. Authors RJS and VME wrote, reviewed, and edited the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

Climate change poses a significant threat to insect populations, with rising temperatures potentially affecting their survival, fecundity, and overall reproductive success. This study investigates the impact of elevated temperature on the reproductive success of *Spodoptera frugiperda* (fall armyworm), a highly destructive and invasive pest. Newly emerged adult moths were exposed to a single heat stress event at 42°C for 2 or 6 hours, simulating extreme summer conditions. Fecundity

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and hatching percentage were measured to assess reproductive performance under thermal stress. The results revealed a significant impact of temperature on both fecundity and hatching percentage. Fecundity was significantly reduced to 1159.5 ± 35.6 eggs when adults were exposed to 42°C for 2 hours, compared to the control group at 27°C, which exhibited a fecundity of 1376.8 ± 30.9 eggs. Interestingly, a recovery was observed in the 6-hour exposure group, where fecundity increased to 1448.7 ± 25.5 eggs, comparable to the control. In contrast, hatching percentage showed a decline under prolonged heat exposure. While the control group and 2-hour exposure group had hatching percentages of 93 ± 1.2% and 90.5 ± 0.9%, respectively, a significant reduction to 78.2 ± 0.9% was observed after 6 hours at 42°C. These findings highlight the potential for heat stress to impair reproductive output in *S. frugiperda*, with implications for population dynamics under climate change. The study provides critical insights into how brief periods of extreme temperatures can affect pest populations, informing pest management strategies in the context of global warming.

Keywords: Fall armyworm; Spodoptera frugiperda; elevated temperature; fecundity; hatching percentage; climate change.

1. INTRODUCTION

Climate change is one of the most critical global challenges, significantly threatening the survival of all living organisms. Its effects include the greenhouse effect, rising temperatures, erratic rainfall, severe droughts, and more. The Intergovernmental Panel on Climate Change (IPCC) projects that global average surface temperatures could increase by 1.5 to 4.5°C by the end of this century, with even a modest rise of about 0.6°C posing risks to all forms of life, including insects. India, characterized by diverse weather patterns, topography, and distinct seasonal variations, is particularly vulnerable to these climatic shifts. Tropical regions like India are anticipated to face extreme temperatures exceeding 45°C, especially in the northern areas during summer. By 2070, the average temperature in India is expected to rise by 1.7°C during the Kharif season and 3.2°C during the Rabi season [1]. Temperature is a critical environmental factor influencing insect physiology and behavior [2], with various aspects of insect growth, development, metabolism, and other physiological processes regulated by a species-specific temperature range. The developmental threshold temperature, essential for completing development, is a fundamental aspect of insect biology, typically adapted to local thermal conditions [3]. Even a 2°C increase in temperature could result in one to five additional generations per season in the life cycle of insects [4]. Although temperature generally has a linear relationship with the rate of insect growth and development, extreme temperatures can cause a decline in this rate, leading to an asymmetrical response curve [2]. Insects, being ectotherms, are highly susceptible to elevated temperatures, which can cause internal body temperatures to reach lethal levels [5]. Warmer temperatures associated with climate change have the potential to significantly impact insect population dynamics by affecting survival, fecundity, and dispersal.

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a highly destructive, polyphagous pest, originally native to the tropical and subtropical regions of the Americas. Known for its considerable egg-laying capacity and exceptional flight abilities, this species poses a significant threat to agriculture [6]. Invasive species like the fall armyworm often demonstrate a remarkable ability to adapt to new environments, which plays a critical role in their successful spread [7]. Although initially restricted to the Americas, the fall armyworm began invading several African countries in 2016, posing a significant risk to agricultural sustainability, especially in Sub-Saharan Africa. The pest was first detected in India in maize fields in Karnataka in May 2018 [8]. Highly polyphagous, it feeds on 353 plant species, causing extensive damage to crops such as maize, sorghum, soybean, and cotton [9,10,11]. In countries like Ghana and Zambia, yield losses attributed to the fall armyworm range between 22% and 67% [12], resulting in annual crop losses of 4.1 to 17.7 million tonnes across Africa [13]. The pest's ability to migrate long distances, coupled with increased globalization, has facilitated its spread to new regions [14]. Moreover, its high fecundity, with over 1000–1500 eggs per female, and its broad host range contribute to its successful establishment and the extensive crop damage observed in newly invaded areas [15].

Temperature impacts on insects are often investigated by subjecting organisms to repeated

heat stress, which has been shown to influence developmental duration, fecundity, and longevity [16]. However, brief periods of high temperature, lasting only a few hours, can still adversely affect reproductive traits, which are particularly vulnerable, thereby impacting the population dynamics of insects. Among various life stages, adults tend to be the most tolerant to thermal stress, but they are still susceptible to carry-over effects in their offspring. Reduced reproductive fitness in adults and their progeny may result from a single heat event affecting either parental sex. Notably, male insects are often more vulnerable to heat shock than females, as observed in species like *Cnaphalocrocis medinalis* [17], *Trialeurodes vaporariorum*, and *Bemisia tabaci* [18]. This vulnerability in males can lead to a significant decline in female fecundity [19]. Conversely, female adults are more sensitive to thermal stress in species such as *Corythucha ciliata* [20] and *Bradysia odoriphaga* [21]. Although many studies have focused on the developmental impairments in insects exposed to thermal stress, there are relatively few reports addressing the effects of high temperature on reproductive success, specifically fecundity and egg-hatching rates, in *S. frugiperda*. To address this gap, we have conducted this study to assess the impact of elevated temperature on the reproductive success of *S. frugiperda*, with a focus on fecundity and hatching percentage. The findings of this research will provide valuable insights into the effects of climate change on pest population dynamics, which could inform strategies for better pest management under changing environmental conditions.

2. MATERIALS AND METHODS

2.1 Rearing of Insects

The larvae of *S. frugiperda* were reared in the laboratory using baby corn as a food source. Pupae were sorted based on sex and placed in individual vials until adult emergence [22]. The insects were maintained under controlled environmental conditions, with a 12-hour light/12-hour dark photoperiod, a temperature of 27° ± 1°C, and relative humidity (RH) of 65% ± 5%. The rearing took place in the Insect Physiology and Molecular Biology Laboratory, Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi. After the adults emerged, they were provided with a 10% honey solution, offered on cotton pads in small Petri dishes.

2.2 Experimental Setup

The study examined the effects of high-temperature events on the fecundity and hatching percentage of *S. frugiperda* adults by exposing newly emerged males and females (≤ 24 hours old) to a single heat stress event of 42°C for either 2 or 6 hours, as outlined by Zhang et al. [23]. The experimental design was based on the summer conditions in Delhi, where maximum temperatures often surpass 40°C for 6-8 hours, with relative humidity ranging from 55% to 65%. These environmental parameters were selected to evaluate how thermal stress impacts the reproductive physiology of *S. frugiperda*. The insects were randomly divided into two groups: one group served as the control and was kept at 27±1°C, while the other group was subjected to 42°C for the specified durations. After the heat exposure, a recovery period of 60 minutes at 27±1°C was provided. To avoid confounding factors related to starvation, a honey solution was supplied to the adults during the thermal stress treatment. The study found that the reproductive fitness of the adults and their offspring was likely reduced due to the single heat event experienced by the parental generation. To further explore these effects, surviving adults were paired for mating in different combinations: control females with control males (CF×CM; 27/27) and heat-stressed females with heat-stressed males (SF×SM; 42/42 for 2 and 6 hours) in specially designed mating jars for fall armyworm. Each treatment combination included 12 male-female pairs, organized into six replications, with two pairs (2:2) per replication, following a completely randomized design (CRD). Post-mating, the insects were allowed to oviposit in mating jars maintained under controlled conditions of 27±1°C, 65±5% relative humidity, and a 14:10 h light: dark cycle.

2.3 Fecundity Assessment

During the oviposition period, the eggs were deposited in clusters on paper strips, muslin cloth, and along the sides of the mating jar. The eggs were collected daily by brushing them off and manually counting them under a stereo-zoom binocular microscope. The fecundity was recorded each day throughout the oviposition period, and the total fecundity for each female was determined by summing the daily counts.

2.4 Hatching/Fertility Percentage

Following egg counting, 100 eggs were selected from each replication of the four treatment

combinations, including the control, across the three different exposure durations, to assess fertility or hatching percentage. The selected eggs were placed in small Petri dishes lined with paper strips, which were moistened with water to prevent desiccation. Egg hatching was monitored twice daily, at 10 a.m. and 5 p.m. The hatching percentage was then calculated using the following formula.

$$Hatching\ \% = \frac{\text{Number of eggs hatched}}{\text{Total number of eggs}} \times 100$$

Data were analyzed using one-way analysis of variance (ANOVA) to evaluate the effect of temperature and exposure duration on fecundity and hatching percentage in *Spodoptera frugiperda*. Differences among treatment means were determined using Duncan's multiple range test (DMRT) at a significance level of $P < 0.05$. Results are expressed as mean ± standard error (SE), with different superscript letters indicating significant differences between means.

3. RESULTS

The analysis of variance (ANOVA) revealed that temperature and exposure duration significantly impacted both the fecundity and hatching percentage of *S. frugiperda*.

3.1 Fecundity

For fecundity, the ANOVA results indicated a significant effect ($F = 15.78$, $df = 2$, $P = 0.000205$). The control group exhibited a fecundity of 1376.833 ± 30.873 eggs, which was significantly higher than the fecundity at 42°C for 2 hours, where it dropped to 1159.5 ± 35.618 eggs. Interestingly, after 6 hours at 42°C, fecundity increased to 1448.667 ± 25.536 eggs, a level that was not significantly different from the control (Fig. 1). Duncan's multiple range test (DMRT) confirmed these findings, showing that fecundity at 42°C for 2 hours was significantly lower than both the control and the 6-hour treatment, while the latter two did not differ significantly from each other (Table 1).

3.2. Hatching Percentage

Similarly, ANOVA showed a significant effect of temperature and exposure duration on the hatching percentage ($F = 39.32$, $df = 2$, $P = 0.00000108$). The control group had a hatching percentage of 93 ± 1.247%, which was not significantly different from the 90.5 ± 0.937% observed at 42°C for 2 hours. However, a significant decline in hatching percentage to 78.167 ± 0.880% was observed after 6 hours at 42°C (Fig. 2). According to DMRT, the hatching percentage after 6 hours at 42°C was significantly lower than both the control and the 2-hour treatment, while the latter two did not differ significantly from each other (Table 1).

Mean ± SE values for fecundity (number of eggs laid) and hatching percentage are shown for three treatments: Control (ambient temperature), 42°C for 2 hours, and 42°C for 6 hours. ANOVA F and P values indicate significance among treatments. Means with the same superscript letter (a, b) within each parameter are not significantly different according to Duncan's multiple range test (DMRT). Lower P values denote greater statistical significance.

Table 1. Effects of temperature stress on fecundity and hatching percentage of *Spodoptera frugiperda*

Parameter	Treatment	Mean ± SE	F value	P value
Fecundity	Control	1376.833 ± 30.873[a]	15.78	0.000205
	42°C, 2 hours	1159.5 ± 35.618[b]		
	42°C, 6 hours	1448.667 ± 25.536[a]		
Hatching percentage	Control	93 ± 1.247[a]	39.32	0.00000108
	42°C, 2 hours	90.5 ± 0.937[a]		
	42°C, 6 hours	8.167 ± 0.880[b]		

4. DISCUSSION

The findings from this study reveal that elevated temperature and exposure duration significantly affect the fecundity and hatching percentage of *Spodoptera frugiperda*. Specifically, short-term heat stress at 42°C for 2 hours resulted in a significant reduction in fecundity (Fig. 1), indicating that brief exposure to high temperatures impairs reproductive output, likely due to stress-induced physiological changes that inhibit egg production. However, an interesting recovery was observed with increased fecundity after 6 hours at 42°C, reaching levels comparable to the control group. This rebound suggests a potential compensatory mechanism or acclimatization, where the moths adapt to prolonged heat exposure and stabilize reproductive capacity despite initial stress.

Conversely, the hatching percentage data highlight that prolonged heat stress is more detrimental to offspring viability than short-term exposure. While exposure to 42°C for 2 hours did not significantly impact the hatching percentage, a substantial reduction was observed after 6 hours (Fig. 2). This decline implies that extended high temperature exposure may damage eggs, disrupting normal embryonic development and resulting in lower hatching success.

The observed patterns in our study align well with existing literature on the effects of heat stress on insect reproduction, highlighting the intricate balance between stress response mechanisms and reproductive fitness. The initial decline in fecundity followed by recovery with longer exposure times suggests the activation of heat shock proteins (HSPs) or other stress-response pathways that may help stabilize reproductive processes during thermal stress. HSPs, particularly HSP70, are known to assist in protein folding and repair, which can mitigate damage caused by high temperatures and restore some reproductive functions. However, this adaptive response in adult fecundity contrasts with the observed reduction in hatching percentages, indicating that while adult moths can acclimate to prolonged heat exposure, their offspring remain vulnerable to thermal stress, impacting overall reproductive success.

Similar patterns have been documented in other insect species, such as mites and fruit flies. For instance, studies on *Tetranychus viennensis* [24], *T. turkestani* [25], *Phenacoccus solenopsis* [19], and *Grapholita molesta* [26] have shown increased fecundity with extended exposure to heat. This variability underscores the complexity of thermal stress responses, which depend heavily on exposure duration and species-specific physiological adaptations. In our study, the reduction in fecundity observed at 42°C for 2 hours reflects findings in insects like *Neoseiulus barkeri* [23], *Helicoverpa armigera* [27], and *Sarcophaga crassipalpis* [28], suggesting that short-term heat exposure triggers an acute stress response that temporarily suppresses reproduction. Conversely, the increase in fecundity at 6 hours, seen in species such as *Opharella communa* [29] and *Liriomyza huidobrensis* [30], may indicate an acclimation period that enables reproductive recovery, highlighting how insects can dynamically adjust to sustained thermal challenges.

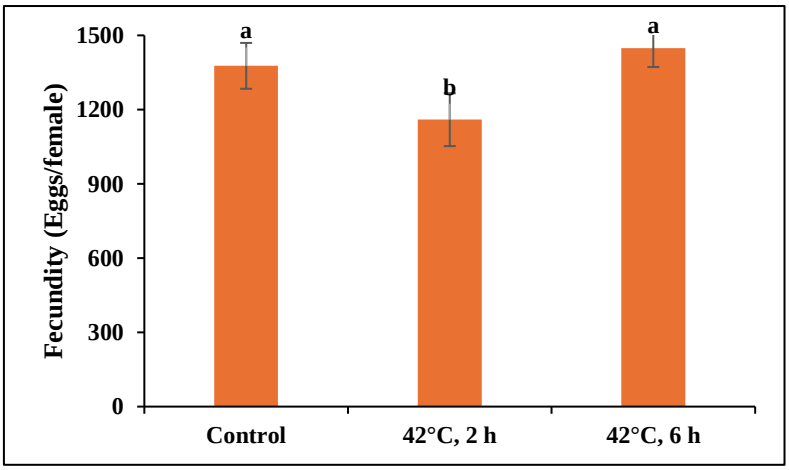

Fig. 1. Effect of temperature stress on the fecundity of *Spodoptera frugiperda*

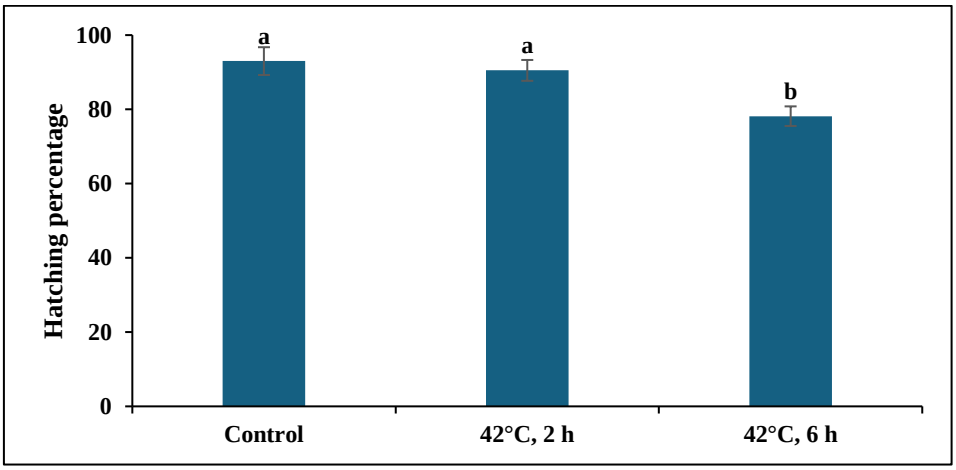

Fig. 2. Effect of temperature stress on the hatching percentage of *Spodoptera frugiperda*

Heat stress impacts on adults can extend to subsequent generations, particularly through effects on egg hatchability. Our findings show that eggs from adults exposed to heat for 2 hours had hatching rates similar to controls, whereas those exposed for 6 hours exhibited reduced hatchability. This reduction may result from the production of sterile eggs, as noted in other studies [28], or due to disruptions in spermatogenesis rather than oogenesis, leading to impaired sperm function [31]. Elevated levels of HSP70, commonly associated with heat stress, have been implicated in reduced hatching percentages [32], supporting the notion that while adult insects may overcome initial heat challenges, their reproductive output can still be compromised at the embryonic stage. In *Helicoverpa armigera*, for example, females subjected to thermal stress produced sterile eggs, emphasizing the critical impact of temperature on reproductive viability [27].

Overall, our results underscore the complex and species-specific effects of heat stress on fecundity and hatching percentage, with significant implications for both immediate and transgenerational reproductive success. This study highlights the need for further research to explore the molecular mechanisms underlying these adaptive responses, such as the role of heat shock proteins, and to assess the impact of repeated or chronic heat exposure on the reproductive fitness of important agricultural pests like the fall armyworm. Understanding these mechanisms will be essential for predicting and managing the impacts of climate change on pest populations, with broader implications for crop protection and agricultural sustainability.

5. CONCLUSION

The study demonstrated that elevated temperatures significantly affect the reproductive success of *Spodoptera frugiperda*. While short-term exposure to 42°C for 2 hours resulted in a notable decline in fecundity, a longer exposure of 6 hours led to a recovery in egg production, indicating potential acclimatization mechanisms. However, this recovery in fecundity did not translate to increased reproductive success, as evidenced by the significant reduction in hatching percentage after 6 hours of heat stress. The results suggest that while adult *S. frugiperda* may adapt to brief heat exposure, their offspring remain vulnerable to the adverse effects of prolonged high temperatures. These findings underscore the importance of considering both immediate and transgenerational impacts of thermal stress on pest populations, particularly in the context of climate change. Future research should explore the molecular and physiological mechanisms driving these responses to develop more effective pest management strategies under changing environmental conditions.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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