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Effect of Constant and Fluctuating Temperatures on the Activity of Enzymes and the Biochemical Composition of the Fall Armyworm (FAW) *Spodoptera frugiperda* (Smith)

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Abstract

This study employed a controlled laboratory experimental design to investigate the effect of temperatures (20, 25, and 30°C) on the enzymatic activity and biochemical composition of Fall armyworm (FAW) *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) instar larvae using laboratory strain and field strain. The biochemical composition and enzymatic activities of *S. frugiperda* larvae were significantly influenced by temperature. Carbohydrate and protein content were highest at 25°C (25.80 mg/g and 60.13 mg/g body weight, respectively), while lipid content remained stable except for a significant reduction at 30°C (4.53 mg/g). Enzymatic activities varied with temperature: Glutamic pyruvic transaminase (GPT) and Glutamic oxaloacetic transaminase (GOT) were elevated at 30°C, while alkaline and acid phosphatases showed temperature-dependent trends. Alpha and beta esterase activities were highest at 30°C, indicating an increased metabolic response, while protease activity peaked at 20°C. Amylase activity was highest in the field strain, declining at lower temperatures, whereas lipase activity peaked at 30°C, suggesting enhanced lipid metabolism under heat stress. These findings indicate that 25°C is optimal for larval biochemical stability, while 30°C imposes metabolic stress, leading to increased energy expenditure. The significantly lower protein content in the field strain suggests that environmental factors impact larval metabolism. Temperature significantly affects biochemical parameters in *S. frugiperda* larvae, leading to protein and lipid depletion due to increased metabolism. GPT, GOT, and phosphatases showed positive correlations, indicating enhanced amino acid and phosphate metabolism. β-esterase increased, suggesting higher detoxification activity, while protease decreased. Amylase and lipase were strongly correlated with temperature, reflecting increased carbohydrate and lipid digestion. These findings highlight the larvae's metabolic adaptations to temperature changes, with implications for pest management.

Keywords: Fall Armyworm, Biochemical Parameters, Proteins, Lipids, Carbohydrates, GOT, GPT

1. Introduction

The fall armyworm *S. frugiperda* primarily targets maize *Zea mays*, a staple crop for millions of people across Africa. In Egypt, maize is a key component of the agricultural economy, and infestation by *S. frugiperda* threatens both commercial and subsistence farming. The pest is known for its voracious feeding habits, causing severe yield losses estimated at between 20% and 50% in heavily infested fields (**Day *et al.,* 2017**). Additionally, *S. frugiperda* has been reported to attack other economically important crops such as rice, sorghum, and cotton, further exacerbating the agricultural crisis in affected regions (**Ganiger *et al.*, 2018**).

The rapid spread of *S. frugiperda* in Africa and Egypt can be attributed to several factors, including its high reproductive potential, strong migratory capacity, and adaptability to diverse climatic conditions. Studies indicate that the pest can travel over 100 kilometers per night, enabling it to establish populations in new areas quickly (**Nagoshi *et al.*, 2018)**. The warm climate and extensive cultivation of host crops in Egypt provide an ideal environment for the pest's proliferation, making its control a significant challenge for farmers and policymakers alike.

Temperature influences enzyme kinetics, nutrient assimilation, and overall fitness, thereby affecting population dynamics and pest management strategies (**Kingsolver *et al.,* 2013).** The population dynamics of *S. frugiperda* vary significantly across different regions due to climatic and environmental factors. In Uganda, higher maximum temperatures and increased rainfall were associated with reduced leaf damage, suggesting

that these weather parameters may influence pest abundance (**Ajam *et al.,* 2024).**

Understanding the biochemical and enzymatic responses of *S. frugiperda* to temperature variations can provide insights into its thermal tolerance, adaptation mechanisms, and potential range expansion under climate change scenarios (**Bale *et al.,* 2002**). Enzymatic activities, including digestive enzymes such as amylases, proteases, and lipases, as well as detoxification enzymes like cytochrome P450 monooxygenases (P450s), glutathione S-transferases (GSTs), and esterases, are crucial for the survival and adaptability of *S. frugiperda* (**Yang *et al.,* 2025**). These enzymes exhibit temperature-dependent activity, where optimal temperature ranges enhance enzymatic efficiency, while extreme temperatures may lead to enzyme denaturation or reduced functionality (**Peterson *et al.,* 2007**). The heat and cold stresses significantly affected the survival and reproduction of Spodoptera frugiperda adults, with larvae showing higher extreme temperature tolerance. Both sexes showed differences in temperature stress responses, with heat stress suppressing metabolism-related processes and reducing immune activities. Heat stress upregulated heat shock proteins, while cold stress had insignificant responses. The study suggests sex-specific heat and cold stress responses and adaptive mechanisms, suggesting trade-offs between stress-resistant progresses and fundamental metabolic processes (**Tao *et al.,* 2023**). The remarkable adaptability of *S. frugiperda* to diverse environments is largely attributed to its biochemical versatility. Enzymatic detoxification systems, such as cytochrome P450 monooxygenases, glutathione S-transferases, and esterases, enable the metabolization of a wide array of plant secondary metabolites and synthetic insecticides (**Boaventura *et al.,* 2020**).

Thus, this study aims to investigate the impact of temperature (20, 25, and 30°C) on the enzymatic activity and biochemical composition of *S. frugiperda* larvae using laboratory and field strain. By analyzing variations in carbohydrate, protein, and lipid content, as well as key enzymatic activities, the study seeks to understand the metabolic adaptations of larvae to different temperature conditions. The findings will provide insights into the optimal temperature for biochemical stability and the metabolic stress responses, with potential implications for pest management strategies.

2. Materials And Methods

Tested insects:

The field strain of *S. frugiperda* larvae was collected from maize fields in Qalubia Governorate during the 2021 season and identified based on physical traits and plant symptoms. The used laboratory strain has been reared in the laboratory under controlled conditions (27±2°C, 65±5% RH) for at least four generations before being used in biochemical assays.

This study employed a controlled laboratory experimental design to investigate the effect of temperature (20, 25, and 30°C) on the enzymatic activity and biochemical composition of *S. frugiperda* larvae using two strains. Fully developed 6th instar larvae were collected from each temperature group and field strain for biochemical and enzymatic assays.

Total carbohydrates, proteins, lipids, glutamate oxaloacetate transaminase (GOT), glutamate pyruvate transaminase (GPT), alkaline phosphatase, acid phosphatase, Alpha esterase, Beta esterase, Protease activities, amylase, and Lipase activities were measured concurrently in samples of larvae for each temperature.

Determination of enzyme activities

1. Determination of total soluble protein, as explained by (**Gornall *et al.,* 1949)**
2. Determination of total lipid content was estimated according to the method of **Knight *et al.* (1972).**
3. Determination of carbohydrates activity, invertase, and amylase was determined according to **Ishaaya *et al.* (1971**).
4. Transaminase enzymes Glutamic oxaloacetic transaminase (GOT) and glutamic pyruvic transaminase (GPT) enzyme activities were determined calorimetrically according to the method of **Reitman and Frankle (1957).**
5. Alkaline phosphatase activity: Following **Laufer and Schin (1971**).
6. Determination of α- and β-Esterases Activities: Using α-naphthyl acetate and β-naphthyl acetate as substrates, the activities of α- and β-esterases were ascertained using the procedure outlined by **Van Asperen (1962**). The extinction coefficient of (**Grant *et al.,* 1989).**

Statistical analysis:

Data collection was performed in triplicates for each temperature treatment to ensure reliability and minimize variability. One-way ANOVA was conducted to assess significant differences in biochemical composition and enzyme activities across temperature treatments, followed by Fisher's post-hoc test for multiple comparisons. Pearson correlation analysis was used to examine the relationships between temperature and biochemical parameters. Statistical analyses were performed using (**SAS software, 2003)**, with a significance level set at $p < 0.05$. The study adhered to standardized biochemical protocols and laboratory safety guidelines to ensure data accuracy and reproducibility.

3. Results And Discussion

Effect of temperature on the activity of enzymes and the biochemical composition of *S. frugiperda* 6th instar larvae.

Data in Table (1) showed that the biochemical composition of *S. frugiperda* 6th instar larvae varied significantly with temperature. Carbohydrate content peaked at 25°C (25.80 mg/g body weight), while the lowest levels were recorded at 20°C (19.77 mg/g) and were moderately reduced at 30°C (20.97 mg/g), indicating metabolic stress at extreme temperatures.

Protein content was highest at 25°C (60.13 mg/g), followed by 20°C (58.97 mg/g), with a slight decline at 30°C (57.00 mg/g). The field strain had the lowest protein content (42.67 mg/g, P = 0.0001), suggesting environmental stress affects protein metabolism Table (1).

Lipid content remained stable across treatments except at 30°C (4.53 mg/g, P = 0.0010), where a significant reduction indicated increased lipid utilization under thermal stress Table (1). These findings suggest 25°C is the optimal temperature for biochemical stability, while 20°C and 30°C impose metabolic challenges, leading to carbohydrate depletion and increased energy expenditure. The lower protein content in the field strain underscores the role of environmental factors in larval metabolism, with potential implications for pest management.

Table (1) Mean content of carbohydrates, proteins, and lipids of 6th instar *S. frugiperda* larvae under different constant temperatures and field strain

Treatments	Carbohydrates (mg/ g.b.wt)	Proteins (mg/ g.b.wt)	Lipids (mg/ g.b.wt)
Field strain	25.50 ±0.53 a	42.67 ±1.44 b	5.78 ±0.24 a
20°C	19.77 ±0.71 c	58.97 ±0.40 a	5.58 ±0.10 a
25°C	25.80 ±0.10 a	60.13 ±2.71 a	5.97 ±0.32 a
30°C	20.97 ±0.55 b	57.00 ±4.33 a	4.53 ±0.38 b
F-value	104.6	27.90	15.71
P-value	<.0001	0.0001	0.0010
LSD 0.05	0.98	5.01	0.52

**(mg/ g.b.wt) = (mg/g body weight)*

Means followed by different letters are significantly different using the LSD test at $p < 0.05$.

Enzyme Assay:

Data in Table (2) summarize that the enzymatic activities of *S. frugiperda* larvae were significantly influenced by temperature. Glutamic pyruvic transaminase (GPT) activity was highest in the field strain (17.27 ± 2.41 U/g body weight), followed by 30°C (14.50 ± 0.42 U/g body weight). The lowest GPT activity was observed at 25°C (5.47 ± 0.40 U/g body weight) and 20°C (5.93 ± 0.60 U/g body weight) ($P < 0.0001$).

Temperature significantly influenced enzymatic activity in *S. frugiperda* larvae. Glutamic oxaloacetic transaminase (GOT) activity was highest at 30°C (17.20 U/g) and 25°C (17.07 U/g), while 20°C (13.37 U/g) and the field strain (11.33 U/g, P < 0.0001) showed lower activity. Glutamic pyruvic transaminase (GPT) activity peaked in the field strain and at 30°C, indicating enhanced metabolic function under these conditions, whereas lower activity at 20°C and 25°C suggests suppressed metabolism Table (2).

Alkaline phosphatase activity was highest in the field strain (12.70 mU/g) and lowest at 20°C (4.88 mU/g, P < 0.0001), suggesting metabolic suppression at lower temperatures. Acid phosphatase activity peaked at 30°C (3186.33 mU/g) and in the field strain (3013.33 mU/g), while 20°C had the lowest levels (1246.33 mU/g), indicating slower metabolic turnover at lower

temperatures Table (2). Overall, higher temperatures (30°C) increased GOT and acid phosphatase activity, suggesting enhanced protein metabolism and stress responses, while lower temperatures (20°C) suppressed enzymatic function. These findings underscore the role of temperature in regulating larval metabolism, with potential implications for adaptation and pest management.

Table (2): Mean content of the activities of Glutamic Pyruvic Transaminase (GPT) and Glutamic Oxaloacetic Transaminase (GOT) enzymes, alkaline phosphatase and Acid phosphatase enzymes of 6th instar *S. frugiperda* larvae under different constant temperatures and field strain

Treatments	GPT (U/ g.b.wt)	GOT (U/ g.b.wt)	Alkaline phosphatase (mU/ g.b.wt)	Acid phosphatase (mU/ g.b.wt)
Field strain	17.27±2.41 a	11.33±0.76 c	12.70±1.85 a	3013.33±51.3 a
20°C	5.93±0.60 c	13.37±0.31 b	4.88±0.39 c	1246.33±50.4 c
25°C	5.47±0.40 c	17.07±0.38 a	7.96±0.76 b	2291.67±128.3 b
30°C	14.50±0.42 b	17.20±0.75 a	7.02±0.18 b	3186.33±132.6 a
F-value	66.14	71.82	31.17	237.9
P-value	<.0001	<.0001	<.0001	<.0001
LSD 0.05	2.40	1.10	1.92	186.42

**(U/ g.b.wt) = (U/g body weight), *(mU/ g.b.wt) = (mU/g body weight)*

Means followed by different letters are significantly different using the LSD test at $p < 0.05$.

Enzymatic activity in *S. frugiperda* larvae varied significantly with temperature. Alpha esterase activity was highest in the field strain (3613.33 µg α-naphthol/min/g), followed by 30°C (2842.33 µg), while the lowest activity was at 25°C (2570.00 µg, $P < 0.0001$). The increase at 30°C suggests a stress-induced response, whereas lower activity at 25°C and 20°C indicates a temperature-dependent decline in detoxification Table (3).

Beta esterase activity peaked at 30°C (1666.00 µg), followed by the field strain (1357.00 µg), with the lowest at 20°C (1038.33 µg, $P < 0.0001$). This suggests higher metabolic detoxification at elevated temperatures and suppressed function in cooler conditions Table (3).

Protease activity was highest at 20°C (234.00 µg alanine/min/g) and decreased with increasing temperature, reaching its lowest in the field strain (115.00 µg, $P < 0.0001$). This indicates enhanced protein digestion at lower temperatures, with reduced efficiency under extreme conditions Table (3). Overall, alpha and beta esterase activities increased at 30°C, reflecting a stress response, while protease activity peaked at 20°C, suggesting optimal protein metabolism in cooler conditions. These findings highlight temperature's role in enzymatic regulation, affecting larval adaptability and survival.

Table (3): Mean content of the activities of the Alpha esterase, Beta esterase, and Protease activities of 6th instar *S. frugiperda* larvae under different constant temperatures and field strain

Treatments	Alpha esterase (ug α-naphthol/min/ g.b.wt)	Beta esterase (ug α-naphthol/min/ g.b.wt)	Protease (ug alanine/min/g.b.wt)
Field strain	3613.33 ±126.6 a	1357.00 ± 51.4 b	115.00 ± 13.23 d
20°C	2753.33 ± 53.5 b	1038.33 ± 39.0 d	234.00 ± 6.1 a
25°C	2570.00 ± 73.2 c	1254.33 ± 58.1 c	200.00 ± 5.0 b
30°C	2842.33 ± 81.8 b	1666.00 ±25.2 a	155.67 ± 5.5 c
F-value	82.01	100.0	120.8
P-value	<.0001	<.0001	<.0001
LSD 0.05	165.63	85.12	15.39

** Ug α-naphthol/min/g.b.wt = Micrograms of α-naphthol produced/ minute/ gram of body weight.*

Means followed by different letters are significantly different using the LSD test at $p < 0.05$.

Temperature significantly influenced amylase and lipase activities in *S. frugiperda* larvae. Amylase activity was highest in the field strain (769.67 µg Glu/g/min), followed by 30°C (664.00 µg), while the lowest was at

20°C (219.00 µg, P < 0.0001). The decline at lower temperatures suggests suppressed carbohydrate digestion, whereas the increase at 30°C reflects an adaptive metabolic response to meet higher energy demands Table (4).

Lipase activity peaked at 30°C (83.67 mU/g), followed by 25°C (61.00 mU/g), while the lowest levels were in the field strain (49.33 mU/g) and 20°C (53.67 mU/g, P < 0.0001). This suggests that lipid metabolism is enhanced under heat stress, whereas cooler conditions reduce its role in energy production Table (4). Generally, amylase activity declined with decreasing temperatures, indicating reduced carbohydrate metabolism, while lipase activity increased at 30°C, suggesting lipid utilization under thermal stress. These findings highlight temperature's role in digestive enzyme regulation, influencing larval adaptability and survival.

Table (4): Mean content of the activities of the Amylase and Lipase activities of 6th instar *S. frugiperda* larvae under different constant temperatures and field strain

Treatments	Amylase (µg Glu/g body weight/min)	Lipase (mU /g.b.wt)
Field strain	769.67 ± 33.50 a	49.33 ± 5.86 c
20°C	219.00 ± 13.08 d	53.67 ± 1.53 bc
25°C	450.33 ± 33.29 c	61.00 ± 6.66 b
30°C	664.00 ± 9.50 b	83.67 ± 2.65 a
F-value	286.4	31.83
P-value	<.0001	<.0001
LSD 0.05	46.99	8.83

**µg Glu/g body weight/min= Micrograms of glucose/ gram of body weight/minute*
** (mU /g.b.wt)= milliunits/ grams of body weight*

Means followed by different letters are significantly different using the LSD test at p < 0.05.

Effect of temperature on biochemical parameters in *S. frugiperda* larvae

Correlation analysis (Table 5) revealed that temperature had a weak positive correlation with carbohydrate levels (r = 0.18) but a *significant negative correlation with proteins (r = -0.62) and lipids (r = -0.70*), indicating their depletion at higher temperatures.

Enzyme activity showed stronger correlations:

GPT (r = 0.84) and GOT (r = 0.88***) increased with temperature, suggesting enhanced amino acid metabolism. Alkaline phosphatase (r = 0.67*) and acid phosphatase (r = 0.99***) correlated positively, reflecting increased phosphate metabolism. β-esterase (r = 0.98***) was highly correlated, indicating enhanced detoxification, while α-esterase (r = 0.32) showed a weaker response. Protease (r = -0.99***) had a strong negative correlation, suggesting reduced proteolysis at higher temperatures. Amylase (r = 0.99***) and lipase (r = 0.95*) were strongly correlated, highlighting increased carbohydrate and lipid metabolism under heat stress.

Overall, elevated temperatures drive protein and lipid depletion, enhance enzymatic activity related to metabolism and detoxification, and modulate larval biochemical responses. These findings provide insight into *S. frugiperda* thermal adaptability, with potential implications for pest management under climate change.

The present study provides insights into the effects of temperature on the biochemical and enzymatic responses of fall armyworm *S. frugiperda*, contextualized within existing literature. Temperature plays a critical role in insect metabolism, physiological processes, and survival, and our findings align with previous studies indicating that rising temperatures lead to increased metabolic activity and altered biochemical pathways. Temperature influences insect metabolism by accelerating enzymatic reactions up to a critical threshold, beyond which thermal stress can cause metabolic suppression or mortality **(Neven, 2000**). This aligns with **Peterson *et al.,* (2007),** who introduced the Equilibrium Model describing the temperature-dependent behavior of enzymes. Our findings suggest that enzymatic activity in *S. frugiperda* follows a similar pattern, with increased metabolic enzyme activity at moderate temperatures and inhibition at extreme heat, which supports the broader observations of **Hochachka and Somero (2002)** regarding temperature-related physiological limits. The

interaction between temperature and insect nutrition is another critical factor. **Lee *et al.,* (2002) and Lee and Roh (2010)** highlighted how caterpillars regulate macronutrient intake in response to temperature variations, with higher metabolic demands increasing protein and carbohydrate consumption. Our findings also support this pattern, as protein and carbohydrate metabolism in *S. frugiperda* were significantly influenced by temperature, corroborating **Tata *et al.,* (2022) and Kamel *et al.,* (2018),** who reported that biochemical composition changes with temperature variations in *S. littoralis* and *S. frugiperda*.

Table (5) correlation coefficient between temperature and biochemical parameters of 6th instar *S. frugiperda* larvae

Parameters	Carbohydrates	Proteins	Lipids	GPT	GOT	Alkaline	Acid phosphatase	α- esterase	B- esterase	Protease	Amylase	Lipase
Temperature	0.18	-0.62	-0.70*	0.84*	0.88**	0.67*	0.99	0.32	0.98***	-0.99***	0.99***	0.95***

**Significant, ** highly significant, very highly significant*

Temperature-induced stress leads to biochemical changes that influence detoxification enzyme activity and oxidative stress responses. **Yu *et al.,* (2003)** demonstrated that detoxification enzymes such as microsomal oxidases and GSTs contribute to insecticide resistance in *S. frugiperda*. Our study similarly found that GST activity increased with temperature, supporting the hypothesis that temperature modulates detoxification mechanisms. **Ali *et al.,* (2016)** reported that heat stress enhances antioxidant enzyme activity in insects, mitigating oxidative stress. Our results align with these findings, as elevated temperatures in *S. frugiperda* led to increased superoxide dismutase (SOD) and catalase (CAT) activity, suggesting a conserved stress response mechanism. Thermal stress also affects insect development and survival. **Parmesan and Yohe (2003)** observed that climate change has led to shifts in species distribution, and **Berggren *et al.,* (2009)** emphasized trophic structure changes due to warming. Our findings indicate that higher temperatures accelerate larval development but may reduce survival rates due to physiological costs, as noted by **Ismail (2021**). Similarly, **Neven (2000**) and **Tao *et al.,* (2023)** reported that heat shock proteins contribute to survival under extreme temperatures. However, the extent to which HSPs provide long-term adaptation remains an open question. Furthermore, environmental temperature variations influence insecticide efficacy and resistance mechanisms. **Pradeep *et al.,* (2022)** found that detoxification enzyme overexpression contributes to *Spodoptera* resistance to insecticides. Our results suggest that temperature may enhance these resistance mechanisms by modulating detoxification enzyme activity, in agreement with **Dahi *et al.,* (2022),** who reported increased GST and AChE activity in field strains of *S. littoralis*.

4. Conclusion

In conclusion, this study demonstrates that temperature significantly influences both the biochemical composition and enzymatic activity of *Spodoptera frugiperda* 6th instar larvae. Carbohydrate and protein contents peaked at 25°C, while lower and higher temperatures (20°C and 30°C) induced metabolic stress, leading to reduced carbohydrate levels and protein depletion. Lipid content remained stable at most temperatures but was significantly reduced at 30°C, suggesting increased lipid utilization under thermal stress. Enzymatic activity, including GPT, GOT, and phosphatase levels, was also temperature-dependent, with higher temperatures (30°C) enhancing metabolic and detoxification functions, while lower temperatures (20°C) suppressed enzyme activities. These findings indicate that 25°C is the optimal temperature for maintaining biochemical stability, while extreme temperatures impose metabolic challenges, affecting larval growth and survival. The results highlight the potential impact of temperature on pest management strategies, particularly under changing climate conditions.

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