Impact of Variegated Temperature, CO2 and Relative Humidity on Survival and Development of Beet Armyworm *Spodoptera exigua* (Hubner) under Controlled Growth Chamber

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Abstract

Climate change will have a noteworthy bearing on survival, development, and population dynamics of insect pests. Therefore, we contemplated the survival and development of beet army worm, *Spodoptera exigua* under different temperatures, (15˚C, 25˚C, 35˚C, and 45˚C), CO2 (350, 550, 750 ppm) and relative humidity (55%, 65%, 75% and 85%) regimes. Maximum larval and pupal weights were recorded in insects reared at 25˚C. The growth of *S. exigua* was faster at 35˚C (larval period 7.4 days and pupal period 4.5 days) than at lower temperatures. At 15˚C, the larval period was extended for 61.4 days and there was no adult emergence from the pupae till 90 days. The *S. exigua* hatchling was absent at 45˚C. The larval survival ranged from 31.6% - 57.2%, maximum survival was recorded at 25˚C, and minimum at 45˚C. The maximum (84.27%) and minimum adult emergence were recorded in insects reared at 25˚C and 35˚C respectively. Maximum fecundity (384.3 eggs/female) and egg viability (51.97%) were recorded in insects reared at 25˚C. Larval and pupal periods increased with an increase in CO2 concentration. The highest pupal weights (128.6 mg/larva) were recorded at 550 ppm. The highest larval survival (73.50%) was recorded at 550 ppm and minimum (37.00%) at 750 ppm CO2. Fecundity was the highest in insects reared at 550 ppm CO2 (657.4 eggs/female), and the lowest at 750 ppm. Maximum larval and pupal weights were recorded in insects reared at 75% relative humidity (RH). The growth rate of *S. exigua* was faster at 85% RH than at lower RH. The larval survival...
ranged between 40.0% - 58.5%. Maximum adult emergence (88.91%) was recorded in insects reared at 75% RH and minimum at 85% RH. Maximum fecundity (447.6 eggs/female) and the highest egg viability (72.95%) were recorded in insects reared at 75% and 65% RH respectively. Elevated temperatures and relative moistness will diminish the life cycle, while hoisted CO₂ will drag the life expectancy. Therefore, there is a need for thorough assessment of the impact of climatic factors on the population dynamics of insect pests, crop losses, and sustainability of crop production.

Keywords

*Spodoptera exigua*, Temperature, CO₂, Relative Humidity and Climate Change

1. Introduction

The fifth estimation report of the Inter-Governmental Panel on Climate Change (IPCC Climate Change 2014) reconfirmed that the globally averaged combined land and ocean surface temperature data as calculated by a direct pattern, show a warming of 0.85°C [0.65°C to 1.06°C] over the period of 1880 to 2012. Global atmospheric concentration of CO₂ has increased from a pre-industrial value of 280 ppm to 410 ppm in 2015 (Mauna Loa Observatory: NOAA-ESRL), and is anticipated to double by the end of the 21st century. Numerous earthly, freshwater, and marine species have moved their geographic extents, occasional exercises, locations, bounties, and species communications in light of continuous atmospheric changes (IPCC Climate Change 2014). IPCC 4th Assessment Report to derive linkages of plant and insect growth models to examine likely changes in insect-crop interaction, have been studied separately, and only a few studies have considered them together (Murray et al., 1996; Taylor et al., 2018). Temperature influences the growth rate of insects significantly and has through effects, whereas the effect of high CO₂ is host-interceded and aberrant (Hunter, 2001). It is well known that developmental rates increase with temperature up to certain levels beyond which they usually decrease (Tshiala et al., 2012). The most predicted effects of climate change, i.e., the increase in temperature and CO₂ concentration will have a significant effect on agriculture in general and on herbivore insect populations in particular. Measurement of the connection between insect advancement and temperature is fundamental to foresee populace elements of the insect pests. This increase is likely to affect biota indirectly via climate change, and directly by producing changes not only in plant growth and allocation, but also in plant tissue chemical composition. Numerous types of herbivorous insects will go up against less nutritious host plants under raised CO₂ conditions, which may induce both prolonged larval developmental times and greater larval mortality (Coviella & Trumble, 1991).

The beet armyworm, *S. exigua* (Hübner; Lepidoptera: Noctuidae) is a poly-
phagous insect pest with a worldwide distribution, and is considered a serious pest of vegetables, field, and flower crops (Suenaga & Tanaka, 2000). Diverse host plants could assume a significant role in population increment and flare-ups of polyphagous insect pests (Singh & Parihar, 1988). For example, *S. exigua* can be found on several host plants such as cotton, cruciferous crops, okra, and wheat, but the young larvae of *S. exigua* at first feed extrovertly on chickpea foliage. As the larvae mature, they become solitary and continue to eat, producing large, irregular holes on the foliage (Ahmed et al., 1990; Sharma et al., 2007). *S. exigua* is a migrant species (Mitchell, 1979) that undertakes long distance migration in Asia, Europe, and North America (Feng et al., 2003). Its transitory limit contributes appreciably to population outbursts and encourages the geographic extension of populations (Adamczyk et al., 2003). The effect of climate change on this pest leads to sporadic outbreaks, and since the late instar larvae are difficult to control with insecticides an early forecasting of *S. exigua* is essential for effective intervention. There are many parameters, which add to *S. exigua* variance in the field including: grown-up movement (conceivably from far off populations) and emigration, the quality, availability, distribution, and preference for alternate hosts and the abundance, distribution, or community composition of natural enemies. The role of host plants, in particular food limitation, is important in regulating insect populations (Umbanhowar & Hastings, 2002) as the life-history traits of herbivores may be influenced by variation in host-plant characteristics (Awmack & Leather, 2002).

There is a need to understand the biology of this pest under prime parameters of climate change. The life tables are important tools for understanding the population dynamics of insect pests and for explaining the effects of various parameters on the development, endurance, and reproduction of insect pest populations. Variation of life table parameters of lepidopterans (intrinsic rate of increase “rm” and finite rate of increase “k”) with temperature (Hardev et al., 2013), larval host and diet (Sheng, 1994) and eCO2 (Dyer et al., 2013) have been reported. Life table parameters of *S. litura* were altered substantially in peanut (Tuan et al., 2013) and in non-*Bt* cotton (Prasad & Sreedhar, 2011) with change in temperature. Studies analyzing variation of life table parameters with both temperatures, RH and CO2 haven’t been attempted. Subsequently, the present studies were conducted under controlled growth chamber in order to predict the pest status during near future (NF) and distant future (DF) under different climate change scenarios.

### 2. Materials and Methods

The current studies on the consequence of different temperature, relative humidity and CO2 regimes on survival and development of beet army worm *S. exigua* were conducted in insect bioassay laboratory at the International Crops Research Institute for the Semi Arid Tropics (ICRISAT), Patancheru, Hyderabad during August 2014 to October 2014. The protocols used in understanding these interactions are described below.
**Maintenance of insect cultures**

**Beet armyworm Spodoptera exigua (Lepidoptera: Noctuidae)**

The insect culture was initiated by collecting the larvae of *S. exigua* from the chickpea fields and reared on the artificial diet for one generation before being acquainted into the research laboratory culture to avoid contamination with the nuclear polyhedrosis virus, bacteria, or fungi. The *S. exigua* neonates were reared in groups of 200 to 250 in 200 mL plastic cups (coated with 2 to 3 mm layer of artificial diet on the bottom and sides) on chickpea-based semi-synthetic artificial diet (Armes et al., 1992) for five days.

After five days, the larvae were individually transferred to 6-cell well plates (each cell well 3.5 cm in diameter and 2 cm depth) containing 7 mL diet (sufficient till pupation). Pupae were surface sterilized with 2 percent sodium hypochlorite and were placed in groups of 50 in plastic jars containing moistened vermiculite for adult emergence. Adults were collected with the help of plastic vials and ten pairs were released in an oviposition cage (30 × 30 × 30 cm) having nappy liners (soft cotton cloth pieces) for egg laying. Adults were provided with 10 percent sucrose in a cotton swab as food in a petri plate. The nappy liners were removed daily and eggs were washed in 2 percent sodium hypochlorite, air dried and placed inside the plastic cups. After egg hatching, the neonates were transferred to the plastic cups containing artificial diet.

**Artificial diet for rearing *S. exigua***

For preparing the chickpea based diet for insect culture, all the ingredients (Armes et al., 1992; Jaba et al., 2017) (Table 1) were weighed separately. The ingredients of fraction A and water (W₁) were mixed thoroughly in a large bowl of 2 L capacity by using a hand mixer and the fraction B along with the yeast was boiled in a saucepan on a hot plate. After boiling, the fractions A and B were blended in an industrial blender. This semi-cooled diet was poured into trays or 250 mL plastic cups (0.5 cm thin layer) and allowed to cool under a laminar flow for one hour. Plastic cups were covered with lids, whereas the, trays were wrapped with polythene sheets to avoid contamination. Nearly 300 mL diet was sufficient to rear 30-neonate larvae up to pupation.

**Effect of climatic factors on survival and development of beet armyworm, *S. exigua***

The endurance and development of beet armyworm, *S. exigua* was studied in four different growth chambers for varied parameters *viz.*, temperature (15˚C, 25˚C, 35˚C, and 45˚C), RH (25%, 50%, 75%, and 95%), and CO₂ concentration (350, 550 and 750 ppm). For studying the effect of temperature, the relative humidity was maintained at 65 percent throughout the development period. The effect of CO₂ and RH was studied by keeping the temperature constant at 27˚C throughout the experiment. One day old early neonate larvae were transferred individually in 25 cell well plates with chickpea flour based semi-synthetic diet and the cell wells were covered with thin food wrapping cover to avoid the neonates from escaping. There were five replications for each treatment and in each replication 50 neonates were released in a completely randomized design.
Table 1. Composition of artificial diet for rearing *H. armigera* larvae.

| Ingredients                        | Quantity |
|------------------------------------|----------|
| **Fraction A**                     |          |
| Chickpea flour                     | 75.0 g   |
| L-ascorbic acid                    | 1.175 g  |
| Sorbic acid                        | 0.75 g   |
| Methyl-4-hydroxy benzoate          | 1.25 g   |
| Aureomycin                         | 2.875 g  |
| Yeast                              | 12.0 g   |
| Formaldehyde (40%)                 | 1.0 ml   |
| Vitamin stock solution             | 2.5 ml   |
| Water (W₁)                         | 112.5 ml |
| **Fraction B**                     |          |
| Agar-Agar solution                 |          |
| Agar-Agar                          | 4.325 g  |
| Water (W₂)                         | 200 ml   |

In order to maintain the fixed parameters, the growth chambers were monitored daily for temperature, CO₂ and RH. For elevated CO₂ experiment, the gas was maintained at set levels using manifold gas regulators, pressure pipelines, solenoid valves, rotameters, sampler, pump, Desktop Linked Program Logic Control, CO₂ gas flow analyzer, and Supervisory Control and Data Acquisition System. The uniformity of the CO₂ was maintained by pumping CO₂ diluted with air by an air compressor. The air was sampled from the center point of the chamber through a coiled copper tube that could be adjusted to different heights for insect cultures on artificial diets. The equipment was monitored, but the CO₂ control in the incubators was fully automatic, and the desired CO₂ level was maintained throughout the experimental period. The carbon dioxide was supplied through two and four cylinders (15 liters capacity) respectively for 550 ppm and 750 ppm.

After one week of initiating the experiment, the utilized diet was replaced with fresh diet. Observations were recorded on larval survival and larval weights at fourth instar/prior pupation. Observations were also recorded on larval, pupal periods, percent pupation and adult emergence percentage.

### 3. Statistical Analysis

The data from effect of climatic parameters on growth and development viz., larval weight, larval duration, pupal weight, pupal duration, percent survival and adult emergence of *S. exigua* were subjected to analysis of variance using GenStat 13th edition, while the significance of differences between the genotypic means was judged by the least significant difference at $P = 0.05$. All the treat-
ments were replicated five times \( (n = 5) \). Treatment means were compared and separated using the least significant difference (LSD) at \( P < 0.01 \).

4. Result

In the present study, the observations were recorded on mean larval weight, percent larval survival, larval period, pupal weight, percent pupation, pupal period and percent adult emergence of *S. exigua* at different temperature, RH and CO\(_2\) regimes.

**Effect of temperature on growth and development of *S. exigua***

The larval weights of *S. exigua* differed significantly across different temperature treatments \( (F_4, 12 = 4.4; \ P < 0.001) \). The mean larval weight gain was substantially higher in larvae maintained at 25°C (233.0 mg) and 35°C (204.0 mg) compared to 15°C (209.2 mg). Similar trend was reflected in average per cent survival of larvae \( (F_4, 12 = 6.01; \ P < 0.001) \) reared at 25°C (57.2%) and 35°C (38.4%) as compared to 15°C (31.0%). The total larval development (time taken from egg hatching to pupation) was extended in the culture maintained at 15°C (61.4 days). While, the development period of 16.4 at 25°C was significantly at par with the treatment 35°C (7.4 days) \( (F_4, 12 = 1.72; \ P < 0.001) \). The pupal weights were 107.2 and 109.5 mg at 15°C and 25°C respectively. While the maximum pupal weight (117.5 mg) was recorded at 35°C \( (F_4, 12 = 19.1; \ P < 0.001) \). The pupal periods varied significantly for rest of the treatments. The maximum pupal period was recorded at 15°C (64.0 days) with no adult emergence. While, it was 4.8 days at 25°C and at par with 35°C (3.8 days) \( (F_4, 12 = 0.91; \ P < 0.001) \). The percent adult emergence was highest \( (84.27\%) \) at 25°C followed by 36.77\% (35°C). There was no adult emergence at 15°C and at 45°C only a few adults emerged but failed to mate (Table 2).

**Table 2.** Effect of temperature on survival and development of *S. exigua*.

| Temperature (°C) | Larval weight (mg) | Larval survival (%) | LP | PP | Pupation (%) | PW (mg) | AE (%) | No. of eggs/female | HP | Hatchability (%) | ML | FL |
|-----------------|------------------|---------------------|----|----|-------------|--------|-------|------------------|-----|----------------|----|----|
| 15              | 209.2 (14.4)     | 31.6                | 61.4 | 0.0 | 50.1        | 107.2 (10.3) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 25              | 233.6 (15.3)     | 57.2                | 16.4 | 4.8 | 88.6        | 109.5 (10.4) | 84.2 | 1.8 | 384.3 | 2.4 | 51.9 | 8.2 | 11.1 |
| 35              | 204.2 (14.3)     | 38.4                | 7.4  | 3.8 | 44.9        | 117.5 (10.8) | 36.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 45              | 0.0 (0.7)        | 0.0                 | 0.0  | 0.0 | 0.0         | 0.0 (0.0)  | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| **Mean**        | **161.7 (12.7)** | **31.8**            | **21.3** | **2.1** | **45.9** | **111.4 (10.5)** | **30.2** | **0.4** | **96.0** | **0.6** | **10.9** | **2.2** | **3.1** |
| \( V_F \)       | 58.6             | 118.1               | 24.1 | 71.6 | 126.1       | 78.5 (16.3) | 63.3 | 16.5 | 28.2 | 28.1 | 27.2 | 57.3 | 56.0 |
| \( P_F \)       | <0.001           | <0.001              | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| LSD             | 4.4              | 6.0                 | 1.7  | 0.9 | 8.2        | 19.1 (13.3) | 0.6 | 6.0 | 0.6 | 0.6 | 12.2 | 1.5 | 2.0 |
| \( SE_F \)      | 3.2              | 4.3                 | 1.2  | 0.6 | 5.9        | 14.1 (9.6)  | 0.6 | 3.7 | 0.7 | 13.3 | 1.6 | 2.2 |
| \( CV \ (%)     | 19.6             | 14.4                | 5.9  | 30.9 | 14.8       | 16.9 (35.6) | 155.4 | 48.2 | 119.0 | 121.0 | 72.9 | 71.2 |

LW: Larval weight; LS: Larval survival; LP: Larval period; PP: Pupal period; PW: Pupal weight; AE: Adult emergence, OP: Ovipositional period; HP: Hatchability period; ML: Male longevity; FL: Female longevity.
Effect of relative humidity on survival and development of S. exigua

The temperature for this experiment was fixed at 27˚C and the RH varied from 55% - 85%. Larval weights varied significantly among all the treatments. The larval weights decreased from 284.6 - 154.4 mg with an increase of RH from 55 to 85% (F4, 12 = 32.92; P < 0.001). The maximum larval survival (58.50%) was recorded at 65% followed by 49.33% at 75% RH (F4, 12 = 7.91; P 0.043) and the minimum (40.0%) was recorded at 55% RH. The larval period differed significantly across treatments, but the increase in weights was very narrow with an increase in the humidity levels (Table 3). The maximum pupal weight was recorded at RH 75% (148.2 mg) followed by RH 85% (134.5 mg) and minimum was recorded at 55% RH (108.4 mg) (F4, 12 = 16.21; P < 0.001). There was no significant variation for pupal period across different RH regimes. However significant variation was recorded for percent pupation, for 65% RH (53.5%) followed by RH 75% (44.55) and least percent pupation was observed at 55% RH (26%).

Effect of CO₂ on survival and development of beet armyworm, S. exigua

Larval weights after 10 days of infestation across different levels of CO₂ ranged from 240.0 - 272.7 mg and the detailed summary is presented in (Table 4). The

| RH (%) | LP | LW | LS (%) | PP | PW | Pupation (%) | AE (%) | FE (%) | ME (%) | OP | HP | No. of eggs | Hatching (%) | FL | ML |
|--------|----|----|--------|----|----|--------------|--------|--------|--------|----|----|-------------|--------------|----|----|
| 55     | 14.5 | 225.8 | 40.0 | 4.5 | 108.4 | 26.0 | (30.3) | 77.2 | (65.4) | 39.8 | (39.0) | 37.5 | (37.3) | 1.6 | 2.0 | 217.4 | (12.7) | 51.6 | (42.7) | 11.1 | 9.1 |
| 65     | 16.7 | 284.6 | 58.5 | 5.0 | 110.4 | 53.5 | (47.0) | 82.9 | (72.1) | 23.7 | (28.3) | 31.9 | (34.0) | 2.8 | 3.3 | 439.6 | (20.6) | 72.9 | (58.9) | 12.1 | 9.6 |
| 75     | 13.7 | 174.3 | 48.6 | 6.0 | 148.2 | 44.5 | (41.8) | 88.9 | (71.2) | 45.1 | (42.1) | 43.8 | (41.3) | 3.2 | 3.0 | 447.6 | (20.3) | 60.1 | (51.2) | 10.6 | 8.3 |
| 85     | 12.5 | 154.4 | 41.0 | 4.7 | 134.5 | 39.0 | (38.6) | 76.0 | (61.1) | 30.8 | (33.6) | 45.3 | (42.2) | 2.0 | 3.4 | 428.9 | (20.0) | 63.6 | (54.3) | 10.6 | 8.3 |
| Mean   | 14.3 | 209.8 | 47.0 | 5.0 | 125.4 | 40.7 | (39.5) | 81.3 | (66.2) | 34.9 | (35.8) | 39.6 | (38.8) | 2.4 | 2.9 | 383.7 | (18.4) | 61.9 | (51.8) | 8.8 | 11.1 |

| Vr  | 50.2 | 32.0 | 4.1 | 3.0 | 14.5 | 8.2 | 0.4 | 3.9 | 1.0 | 6.1 | 4.8 | 4.0 | 2.3 | 0.8 | 0.74 |
| Fpr | <0.001 | <0.001 | 0.043 | 0.083 | <0.001 | 0.006 | 0.713 | 0.046 | 0.402 | 0.003 | 0.008 | 0.017 | 0.100 | 0.500 | 0.530 |
| LSD | 1.3 | 32.9 | 7.9 | 1.2 | 16.2 | 7.8 | 19.6 | 9.7 | 11.5 | 0.8 | 0.7 | 5.5 | 13.0 | 2.0 | 2.3 |
| SE±  | 0.5 | 14.2 | 3.5 | 0.5 | 7.1 | 3.4 | 8.6 | 4.3 | 5.1 | 0.4 | 0.3 | 2.6 | 6.3 | 1.0 | 1.16 |
| CV (%) | 6.2 | 9.8 | 11.4 | 14.2 | 8.1 | 12.4 | 18.5 | 17.0 | 18.5 | 38.9 | 29.4 | 32.5 | 27.5 | 25.5 | 23.5 |

LP: Larval Period; PP: Pupal Period; PW: Pupal Weight; AE: Adult Emergence; FE: Female Emergence; ME: Male Emergence; OP: Ovipositional Period; HP: Hatchability Period; FL: Female Longevity; ML: Male Longevity.
Table 4. Effect of varied CO2 on the survival and development of S. exigua.

| CO2 (PPM) | LW (mg) | LP | LS (%) | PP | PW (mg) | Pupation (%) | AE (%) | ME (%) | FE (%) | OP | Fecundity | Incubation period | Viability (%) | ML | FL |
|-----------|---------|----|--------|----|---------|--------------|--------|--------|--------|----|-----------|-------------------|---------------|----|----|
| 350       | 272.1   | 13.2 | 52.5 (46.4) | 5.5 | 121.2   | 69.8 (58.2) | 76.8 (62.9) | 46.3 (42.8) | 30.5 (33.1) | 2.8 | 384.3 (18.0) | 3.3 | 79.3 (63.5) | 9.5 | 12.2 |
| 550       | 223.0   | 15.5 | 73.5 (59.0) | 6.2 | 128.6   | 93.7 (75.9) | 78.7 (63.5) | 42.8 (40.8) | 35.8 (36.6) | 2.7 | 657.4 (25.0) | 2.8 | 88.9 (71.2) | 11.2 | 12.9 |
| 750       | 223.5   | 15.5 | 37.0 (37.4) | 6.0 | 124.3   | 85.0 (67.3) | 59.9 (51.0) | 30.3 (33.2) | 29.5 (32.5) | 2.2 | 99.0 (9.2) | 2.5 | 17.5 (20.8) | 5.1 | 9.0 |
| Mean      | 240.0   | 14.7 | 54.3 (47.6) | 5.9 | 120.0   | 82.9 (67.2) | 71.8 (59.1) | 39.9 (38.9) | 32.0 (34.1) | 2.5 | 17.2 | 2.8 | 51.8 | 8.6 | 11.3 |
| Vr        | 2.2     | 2.5 | 117.3 | 0.5 | 0.5     | 4.2 (1.1)   | 2.0 (0.3)   | 1.7 (1.7)   | 13.0 (1.2) | 1.2 | 90.0 | 20.3 | 10.7 |
| Ppr       | 0.1     | 0.1 | <0.001 | 0.595 | 0.613 | 0.071 | 0.384 | 0.210 | 0.708 | 0.201 | <0.001 | 0.308 | <0.001 | <0.001 | <0.001 |
| LSD       | 0.0     | 2.8 | 3.4 | 1.7 | 0.0 | 14.9 | 22.9 | 12.2 | 12.6 | 0.7 | 6.4 | 1.0 | 8.4 | 2.0 | 1.8 |
| SE±       | 0.2     | 1.1 | 1.4 | 0.7 | 0.0 | 6.1 | 22.9 | 5.0 | 5.1 | 0.3 | 3.0 | 0.5 | 4.0 | 0.9 | 0.8 |
| CV (%)    | 15.7    | 11.0 | 4.2 | 17.1 | 8.2 | 12.8 | 22.4 | 18.2 | 21.5 | 29.9 | 39.6 | 39.8 | 17.4 | 25.7 | 17.6 |

LW: Larval Weight; LP: Larval Period; LS: Larval Survival; PP: Pupal Period; PW: Pupal Weight; AE: Adult Emergence; ME: Male Emergence; FE: Female Emergence; OP: Ovipositional Period; HP: Hatchability Period; ML: Male Longevity; FL: Female Longevity.

The relative growth rate of larvae was significantly higher on diet maintained at ambient CO2. The maximum larval weight (272.1 mg) was recorded at 350 ppm followed by 223.5 mg (750 ppm) and minimum was recorded at 550 ppm (223.0 mg) (F4, 12 = 0.065, P 0.18). The higher per cent larval survival was recorded in 550 ppm (73.50) followed by 350 ppm (52.5) CO2 conditions (F4, 12 = 3.46; P < 0.001). The total larval period (time taken from hatching to pupation) 15.5 days (F4, 12 = 2.81; P 0.15) at elevated CO2 (750 ppm and 550 ppm) was significantly at par with 350 ppm (13.25 days). The mean pupal weight varied significantly across CO2 concentrations; it was highest at 550 ppm (128.6 mg) followed by 750 ppm (124.0 mg). The minimum pupal weight was recorded at 350 ppm (121.0 mg) (F4, 12 = 1.75; P 0.059) (Table 4). The highest percent pupation was recorded at 550 ppm (93.73) and lowest at 350 ppm (69.89). The highest fecundity (657.4) and viability (88.96) (F4, 12 = 6.49; P < 0.001) per cent were recorded at 550 ppm while the lowest (99.0; 17.50%) (F4, 12 = 8.49; P < 0.001) were recorded at 350 ppm. There were significant differences among the treatments for both male and female adult longevity. The highest (11.2; 12.9 days) and lowest (5.1; 9.0 days) male and female longevity were recorded at 550 ppm and 750 ppm respectively.

5. Discussion

In this study, we investigated the effect of different temperature, relative humidity and CO2 regimes on survival and development of S. exigua (Table 5).

Effect of temperature on growth and development of S. exigua

Insects are poikilothermic in nature, i.e., cold-blooded, and hence the environment temperature has the greatest effect on insect development rates. In our
Table 5. Effect of temperature, CO₂ and RH on growth and development of S. exigua. Max: Maximum; Min: Minimum.

| Development Index | Temperature (˚C) | CO₂ (ppm) | RH (%) |
|-------------------|-----------------|-----------|--------|
|                   | 15˚C | 25˚C | 35˚C | 45˚C | 350 | 550 | 750 | 55 | 65 | 75 | 85 |
| Fecundity         | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  |
| Egg viability     | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  |
| Larval survival   | -    | Max  | -    | Min  | -    | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  |
| Larval period     | Extended | Shorter | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    |
| Pupal period      | Max  | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    | -    |
| Larval weight     | Max  | -    | -    | Max  | Min  | -    | -    | -    | -    | Max  | Min  | -    | Max  | -    | -    | -    | -    | -    | -    |
| Pupal weight      | Min  | Max  | -    | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  | Min  | Max  |
| Adult emergence   | Max  | Min  | -    | -    | -    | -    | -    | -    | -    | Max  | Min  | -    | Max  | Min  | -    | -    | -    | -    | -    |

In the present study, the beet army worm S. exigua developmental time differed significantly across temperatures. Larvae fed with diet maintained at 35°C exhibited lower larval weight and larval duration as compared to 25°C and 15°C. By and large, higher temperatures result in reduction of duration and development of each biological stage. It is outstanding that the connection between temperature and advancement in insects is straight across the mid-ranges, but becomes sigmoid over the entire temperature range that permits growth and development (Arbab et al., 2006). The metabolic activity of insect body is triggered between 26˚C - 34˚C for enhancing better growth and development. The maximum pupal weight and adult emergence were recorded at 35°C and 25°C respectively. These results are in agreement with (Terblanche et al., 2010; Ehnes et al., 2011) who showed that elevated temperature may also increase the nutrient demands of insects as a result of raised metabolic rates, potentially leading to compensatory feeding as a direct effect of elevated temperature (Levesque et al., 2002); however, this may not always be the case (Addo-Bediako et al., 2002). Survival of insects may also be directly affected by elevated temperatures (Rouault et al., 2006; Friedenberg et al., 2008). The results of present studies are also in corroboration with these reports. The effect of temperature on the survival and development of S. exigua (pupation and per cent adult emergence) across temperatures are shown in Figures 1(a)-(d). Temperature is the most significant factor influencing the growth and development of insects (Bale et al., 2002). The effects of temperature on insects are species specific. Earlier studies have revealed that the growth and development of S. litura was significantly influenced by temperature (Ranga Rao et al., 1989) and CO₂ (Srinivasa Rao et al., 2012) on various hosts. The results of the present study showed that the developmental time of different developmental stages of S. exigua (Egg-adult) declined with increase in temperature. The rate of development was arrested at higher temperatures (45°C), signifying the adverse effects of extreme temperatures on growth of S. exigua, resulting in early mortality of larval population.
Figure 1. (a) Larval, pupal period and adult longevity of S. exigua on artificial diet at different weather variables; (b) Percent larval survival, adult emergence and hatchability of S. exigua under different weather variables; (c) Larval and pupal weights of S. exigua on artificial diet across different Temperatures, RH and CO₂ regimes; (d) Oviposition and fecundity of S. exigua on artificial diet at different Temperatures, RH and CO₂ concentrations.

Effect of CO₂ on survival and development of beet armyworm, S. exigua

In the present study, the insect growth varied significantly across different CO₂ concentrations. The development period was prolonged when the larvae were fed on diet maintained at elevated CO₂ (750 ppm). The mean larval weights were higher at elevated CO₂. The larval development period was prolonged and the pupal weights decreased when S. exigua larvae were reared from hatching to pupation at elevated CO₂ (750 ppm) (Figures 1(a)-(d)). The larval weights and percent adult emergence were lower at elevated CO₂ (750 ppm) as compared to 350 and 550 ppm. It is also tacit that larvae assimilated more but grew slower. The results of this experiment are in corroboration with (Lindroth et al., 1993) who reported that low efficiency of conversion of digested food may result from a requirement of these insects to metabolize digested food in order to produce water. A similar observation was reported on cotton leaf worm by (Agrell et al., 2006). The fecundity of S. exigua was reduced under elevated (750 ppm) CO₂ conditions, and this might be due to lower pupal weights. Relative growth rates of Gypsy moth (Lymantria dispar) were reported to be reduced by 30% in larvae fed on Quercus petraea exposed to high CO₂ (Haettenschweiler & Schafellner, 2004).

Effect of relative humidity on survival and development of beet armyworm, S. exigua

The present studies showed that higher relative humidity hindered the overall growth and development of S. exigua and resulted in lower percent adult emergence (Figures 1(a)-(d)). Better larval growth, larval weight, percent pupation,
pupal weight and maximum adult emergence were recorded between 50% - 75% RH. The results of this experiment are in corroboration with (Li et al., 2014) who found that high humidity may affect the defense system of *S. exigua* larvae, resulting in higher host mortality. The percent adult emergence was also affected by lower humidity (25% RH) which is in agreement with (Wigglesworth, 1984) who reported that low RH resulted in water loss through the egg and pupal membranes which can be detrimental for the survival of holometabolous insects, resulting in desiccation.

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**Conflicts of Interest**

The authors declare no conflict of interest.

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