



## Influence of climate change on tri-trophic interaction in maize (*Zea mays*) ecosystem

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### ABSTRACT

The study was carried out during 2022–23 at University of Agricultural Sciences, Raichur, Karnataka to investigate the influence of climate change in maize (*Zea mays* L.) ecosystems against maize fall armyworm, *Spodoptera frugiperda*; and with a focus on parasitoids, *Trichogramma chilonis* (egg parasitoid) and *Goniozus nephantidis* (larval parasitoid). The study was done under Open Top Chambers (OTCs) with treatments T<sub>1</sub>, Ambient CO<sub>2</sub> at 410 ppm with 31°C (Reference OTC); T<sub>2</sub>, Ambient CO<sub>2</sub> at 410 ppm with a 2°C rise in temperature; T<sub>3</sub>, Elevated CO<sub>2</sub> at 550 ppm with 31°C; T<sub>4</sub>, Elevated CO<sub>2</sub> at 550 ppm with a 2°C rise in temperature and T<sub>5</sub>, Reference (open) field. The results revealed that under elevated CO<sub>2</sub> at 550 ppm + raised temperature at 33°C, the plant height, number of leaves, and chlorophyll content increased along with grain and fodder yield. However, decreased in foliar nitrogen levels of maize leaves forced fall armyworm to eat more plant material to acquire the nutrition required, causing greater crop damage. This led to more larval weight (592.0 ± 1.64 mg) and prolonged larval duration (28.03 ± 0.05 days), while decreasing pupal weight (225.7 ± 6.37 mg), female fecundity (720/female) indicating reduced overall fitness. At the tri-trophic level, both the parasitoids showed reduced performance under climate change conditions. *T. chilonis* had lower success rates in attacking pest eggs (63.16% parasitism, 61.93% emergence) and took longer to develop (11 days). Similarly, *G. nephantidis* produced smaller adults (3.50 mm ± 0.02 mm) with reduced emergence rates (66.07%) due to the compromised quality of their hosts as a result of climate change. This research demonstrates how climate change disrupts natural pest control systems, potentially making crop protection more challenging in the future.

**Keywords:** Climate change, Maize, Natural enemies, *Spodoptera frugiperda*, Tri-trophic interaction

Over the past century, there have been profound shifts in Earth's climate. Many human-induced actions have led to remarkable increases in the levels of carbon dioxide (CO<sub>2</sub>) and other gases in the atmosphere, leading to increased temperatures and changes in precipitation patterns. This climate change represents considerable pressure on living organisms to swiftly adapt to new environmental conditions. Climatic factors, such as CO<sub>2</sub>, temperature, and precipitation, influence plant molecular functions, developmental processes, physiology, and morphology (Gray and Brady 2016). Shifts in plant and animal physiology, behaviour, and phenology, can further reverberate their interaction networks. Modifications in the primary trophic level can lead to alterations in trophic levels, potentially affecting ecosystem services (Dash *et al.* 2017). Increase in temperature and atmospheric CO<sub>2</sub> interrupt the relationships among plants, herbivores, and their associated enemies through complex mechanisms (Dyer *et al.* 2013). For instance, elevated temperature and

CO<sub>2</sub> can stimulate photosynthetic carbon assimilation, decrease nitrogen content, and increase biomass production, which impacts the production of plant nutrients and secondary metabolites and, can modify the multi-trophic interactions via cascading effects through the food chain in the agro-ecosystem (Sun *et al.* 2011a, Robinson *et al.* 2012). Elevated concentrations of atmospheric carbon dioxide, a consequence of anthropogenic global change, may profoundly interfere with tri-trophic interactions. The food availability and quality of herbivores may be affected by the host plant's response to climate change (Berryman 1996). Climate change is expected to strongly reconfigure tri-trophic interactions between plants, insect herbivores, and their enemies (Guyer *et al.* 2021).

In agricultural ecosystems, the dynamics of insect populations are governed by top-down pressures, such as predation and parasitism of herbivores by predators and parasitoids, as well as bottom-up forces, including the regulation of herbivore populations by host plants (Reich *et al.* 2006). Parasitoid efficiency in tri-trophic interactions may be altered by climate change, as parasitoids could also be affected by plant-mediated changes in herbivore hosts (Sun *et al.* 2011b). Studying the impacts of climate change

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at the tri-trophic level provides an opportunity to understand future insect pest scenarios. Hence, to investigate the impact of climate change on elevated CO<sub>2</sub> and temperature, maize was chosen for this study.

Various insect species pose a threat to maize by, inflicting damage that spans from occasional feeding to nearly destroying the plants, resulting in significant yield losses. Among the damaging species, the fall armyworm, *Spodoptera frugiperda* (J E Smith) is the most devastating pest. It is a polyphagous pest that attacks 353 plant species belonging to 76 plant families, mainly Poaceae, Asteraceae and Fabaceae (Montezano *et al.* 2018). However, it is primarily a pest of grasses and prefers maize. Young leaf whorls, ears and tassels are considered the major feed sources causing significant damage to maize, resulting in occasional yield loss (Chormule *et al.* 2019). Therefore, the purpose of this study was to evaluate the effects of CO<sub>2</sub> and temperature-mediated changes in tri-trophic interactions involving maize, fall armyworm, and parasitoids, viz. *Trichogramma chilonis* (Ishii) and *Goniozus nephantidis* (Muesebeck), which is an important step towards understanding the ecological consequences of constantly increasing atmospheric CO<sub>2</sub> concentrations. To date, only few studies have been conducted on the effects of high CO<sub>2</sub> and temperature on fall armyworm and its parasitoids. Therefore, the current study was carried out to acquire better knowledge of the adaptational behaviour of insects under changing climatic conditions.

#### MATERIALS AND METHODS

*Open-top chambers:* The study was carried out during 2022–23 at University of Agricultural Sciences, Raichur, Karnataka (16.2048° N, 77.3341° E; an elevation of 484 m amsl) under Open Top Chambers (OTCs). Elevated CO<sub>2</sub> and temperature (abiotic factors) were considered as the main treatments in the present study. Each OTCs were considered as a treatment for this study and the set of treatments designed as per the recommendations of IPCC (2022) are as follows; T<sub>1</sub>, Ambient CO<sub>2</sub> at 410 ppm with 31°C (Reference OTC); T<sub>2</sub>, Ambient CO<sub>2</sub> at 410 ppm with a 2°C rise in temperature; T<sub>3</sub>, Elevated CO<sub>2</sub> at 550 ppm with 31°C; T<sub>4</sub>, Elevated CO<sub>2</sub> at 550 ppm with a 2°C rise in temperature and T<sub>5</sub>, Reference (open) field. The seeds of the popular maize variety RCMH-4 were dibbled (spacing of 60 × 30 cm) in each OTC with black soil mixed with vermicompost (4 tonnes/ha), and chemical fertilizers (60:26:26 kg/ha) were added according to the recommendations of the University of Agricultural Sciences, Raichur, Karnataka (Anonymous 2021). Each treatment (OTC) included 35 maize plants in different OTCs under standard climate change treatments. Among the 35 plants, 30 plants in each OTC were covered with nylon cages (mesh size of 1.2 mm) to avoid the escape of fall armyworm larvae. The remaining five plants were selected and tagged to observe the growth and physiological parameters, viz. plant height, number of leaves per plant, and chlorophyll content (using a SPAD meter) at 30, 60, and 90 days of plant growth.

Table 1 Measurement of damage as per Davis scale

Scale	Description
0	No visible damage
1	Only pinhole damage on leaves
2	Pinhole and shot hole damage to leaf
3	Small elongated lesions (5–10 mm) on 1–3 leaves
4	Midsized lesions (10–30 mm) on 4–7 leaves
5	Large elongated lesions (>30mm) or small portions eaten on 3–5 leaves
6	Elongated lesions (>30 cm) and large portions eaten on 3–5 leaves
7	Elongated lesions (>30cm) and 50% of leaf eaten
8	Elongated lesions (30 cm) and large portions eaten on 70% of leaves
9	Most leaves with long lesions and complete defoliation observed

Yield parameters, such as cob length and weight, number of rows per cob, test weight, grain yield, and fodder yield, were also recorded to examine the effect of climate change on maize in OTCs.

*Release of fall armyworm inside OTCs:* The maize crop raised in each OTCs when attained 25 days old, second instar fall armyworms were released on each of the 30 maize plants with various climate change treatments mentioned above. The plants were examined daily to document the extent of leaf damage (using the Davis scale) caused by the larvae on each plant until they reached the last instar (Table 1). Later, late instar larvae were collected from each OTCs and placed in plastic jars (10 cm × 10 cm) for further rearing. Sexing was performed at the pupal stage to differentiate between males and females. The weight of the sixth instar, total larval duration, pupal weight, pupal duration, and fecundity of the females were recorded, and the mean was calculated. The F<sub>1</sub> generation of *S. frugiperda* was used for the parasitism study.

*Effect of climate change on T. chilonis mediated by eggs S. frugiperda at tri-trophic level:* To study the parasitism rate of *T. chilonis* on the eggs of fall armyworm obtained from each respective climate change treatment, one adult gravid female of *T. chilonis* was individually placed into glass vials (8 cm height × 2 cm diameter) containing a small egg card (2 cm × 1 cm) made up of freshly collected UV-irradiated *S. frugiperda* eggs (24 h old), and approximately 50 eggs were pasted randomly on a small white card strip smeared with diluted gum, and the vial was plugged with cotton. After 24 h, the parasitoids were removed, and the vials containing parasitized egg cards were then kept in a controlled environmental chamber (25 ± 1°C temperature, 70 ± 5% RH, 14/10 h (L: D) photoperiod) (Tefera *et al.* 2019). Therefore, the total developmental time (egg-to-adult in days), per cent parasitisation [no. eggs parasitized/total no. of eggs × 100], and per cent adult emergence [no. parasitoids emerged/total no. parasitized eggs × 100] were

observed. The experimental set up was replicated four times for each treatment.

**Effect of climate change on *G. nephantidis* mediated by larvae of *S. frugiperda* at tri-trophic level:** The parasitic potential of *G. nephantidis* females was ascertained by exposing an adult gravid female of *G. nephantidis* to the fourth instar larvae of *S. frugiperda* from their respective treatments in a glass test tube (7 cm × 1.5 cm). Each mated female (after completion of pre-oviposition) was exposed to fall armyworm larvae for 48 h. The next day, the same parasitoid female was removed and exposed to a new larva of fall armyworm in the same manner into a new glass tube. During this period, the females were fed on 10% diluted honey solution dipped with cotton, which was used as a plug to avoid its escape, covered with a black muslin cloth, and tied with a rubber band. Every 48 h, the adult female parasitoids were removed and exposed to a new fourth instar fall armyworm larvae until the death of the female. The developmental stages of *G. nephantidis* on *S. frugiperda* were observed under a compound microscope using a very fine needle and moistened brush to observe and determine the number of eggs, grubs, pupae, pupal weight, number of adults emerged, and adult emergence percentage, therefore the parasitic potential of *G. nephantidis* on *S. frugiperda* larvae mediated by elevated CO<sub>2</sub> and temperature at a tritrophic level was determined. The lengths of the various stages (five individuals from each stages) of *G. nephantidis* were measured under a stereo-zoom microscope and the mean was calculated.

**Statistical analysis:** Statistical analysis is a key factor for data analysis and interpretation. SPSS (Version 16.0) was used for the analysis of the data i.e. univariate one-way analysis, F-test and post hoc test such as Duncan Multiple Range Test (DMRT) at 0.01 significance level. Data in numbers and percentage were transformed through square root and arc sine transformations, respectively, using Microsoft-Excel.

## RESULTS AND DISCUSSION

### *Effect of elevated temperature and CO<sub>2</sub> at the first trophic level*

**Plant growth parameters:** Climate change, as indicated by elevated CO<sub>2</sub> levels and rising temperatures, has benefitted the growth of maize crop. Many earlier investigations have found that maize, a C<sub>4</sub> plant, responds positively to CO<sub>2</sub> by demonstrating enhanced growth rates, which is consistent with the present findings. This is supported by the observed acceleration in growth rates under elevated CO<sub>2</sub> at 550 ppm + raised temperature at 33°C in terms of plant height (305 cm/plant) and number of leaves (13.60/plant). The shortest plant height (62.80 cm) was observed in the reference plot with the minimum number of leaves (8.20 leaves/plant). Similar studies by Adishesha *et al.* (2017) and Mounica *et al.* (2020) showed increased growth rates of maize under elevated CO<sub>2</sub> conditions. The total chlorophyll content was positively affected by higher CO<sub>2</sub> concentrations and temperatures compared to the ambient conditions. Elevated CO<sub>2</sub> at 550 ppm + raised temperature at 33°C have also led to higher chlorophyll content (44.28 µg/cm<sup>2</sup>) as compared to the reference plot (39.33 µg/cm<sup>2</sup>) (Table 2). This increase in chlorophyll concentration could be the result of tissues using more carbon, which leads to an increase in chlorophyll content. Many studies on a variety of crops, including Berliner (1915) in (*Bt*) oilseed rape, Sari *et al.* (2008) in *Bacillus thuringiensis*, Miri *et al.* (2012) in cotton crops and Megha (2020) in cowpea, reported an increase in chlorophyll content with increased CO<sub>2</sub> and temperature treatments.

**Yield parameters:** The growth parameters exhibited a favourable pattern alongside the yield measures, leading to higher grain and fodder yields under elevated CO<sub>2</sub> and temperature conditions. Under these conditions, the maximum cob length (21.91 cm), cob weight (270.8 g), and number of seed rows/cob (13.90 rows) were recorded

Table 2 Effect of elevated CO<sub>2</sub> and temperature at the first trophic level (maize)

Treatments	Growth parameters at different DAS		Physiological parameter	Yield parameters						
	Plant height (cm)	Number of leaves/plant	Chlorophyll (µg/cm <sup>2</sup> )	Cob length (cm)	Weight of one cob (g)	Number of seed rows/cob	Test weight (g)	Maize yield/30 plants (kg)	Maize yield (t/ha)	Fodder weight/30 plants (kg)
aCO <sub>2</sub> @410 ppm + 31°C	195.3 <sup>c</sup>	11.33 <sup>c</sup>	37.83 <sup>c</sup>	18.36 <sup>c</sup>	181.7 <sup>d</sup>	12.50 <sup>c</sup>	23.86 <sup>bc</sup>	5.55	10.29	4.05 <sup>c</sup>
aCO <sub>2</sub> @410 ppm + 33°C	209.8 <sup>b</sup>	12.20 <sup>b</sup>	38.51 <sup>c</sup>	20.07 <sup>b</sup>	249.1 <sup>b</sup>	13.00 <sup>bc</sup>	24.55 <sup>ab</sup>	5.79	10.66	4.63 <sup>b</sup>
eCO <sub>2</sub> @550 ppm + 31°C	219.7 <sup>a</sup>	12.67 <sup>ab</sup>	40.06 <sup>b</sup>	21.38 <sup>a</sup>	257.7 <sup>b</sup>	13.50 <sup>ab</sup>	26.04 <sup>a</sup>	6.39	11.77	4.90 <sup>ab</sup>
eCO <sub>2</sub> @550 ppm + 33°C	225.0 <sup>a</sup>	12.87 <sup>a</sup>	41.72 <sup>a</sup>	21.91 <sup>a</sup>	270.8 <sup>a</sup>	13.90 <sup>a</sup>	27.16 <sup>a</sup>	6.90	12.79	5.02 <sup>a</sup>
Reference plot	166.1 <sup>d</sup>	10.67 <sup>d</sup>	36.08 <sup>d</sup>	18.47 <sup>c</sup>	201.8 <sup>c</sup>	12.50 <sup>c</sup>	22.85 <sup>c</sup>	5.26	9.78	3.70 <sup>d</sup>
CV (%)	4.27	2.43	1.21	3.89	3.03	4.08	2.68	-	-	3.64
SEM (±)	3.78	0.13	0.21	0.25	3.15	0.33	0.30	-	-	0.07
CD (p=0.01)	14.03	0.64	1.09	1.43	12.38	0.90	1.55	-	-	0.37

DAS, Days after sowing. Means denoted by the same letters in the vertical column are not significantly different by DMRT multiple range test.

in eCO<sub>2</sub> (Elevated CO<sub>2</sub>) at 550 ppm + raised temperature at 33°C. The highest test weight (27.16 g) and highest grain yield (6.90 kg/30 plants) was recorded under eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C in contrast to the yield in the reference plot which recorded 5.26 kg/30 plants (Table 2). The yield was much higher under eCO<sub>2</sub> than under aCO<sub>2</sub> (Atmospheric CO<sub>2</sub>) conditions. The yield of maize has increased owing to rapid growth and photosynthetic rates. Moreover, the combination of increasing CO<sub>2</sub> concentration and air temperature led to higher grain output and a higher harvest index, as reported by Moya *et al.* (1998). Likewise, Megha (2020) reported that cowpea crops grown under conditions of increasing CO<sub>2</sub> and temperature showed an increase in total chlorophyll as well as growth and yield parameters.

#### *Effect of elevated temperature and CO<sub>2</sub> at the second trophic level*

*Effect on damage intensity by S. frugiperda:* Using the Davis scale, weekly assessments of leaf damage were conducted under various climate change conditions. The highest leaf damage score was 6.36/plant was observed under eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C while the reference plot showed substantially less damage (3.87/plant) (Table 3). These findings unequivocally indicated that maize crops subjected to climate change treatments, which involved elevated levels of CO<sub>2</sub> and temperature, suffered greater damage. The results clearly showed that maize crops grown under climate change treatments that included higher CO<sub>2</sub> and temperature induced more damage (Xie *et al.* 2015). This was attributed to the higher feeding rate of fall armyworm, which is normally associated with the nutritional content of the leaves. Lower nitrogen levels in the elevated

CO<sub>2</sub> and temperature treatments resulted in lower nutritional quality of the leaves. As a result, the fall armyworm feeds more to meet the nutritional requirements for proper growth and development, causing greater crop damage (Pooja 2022). Megha (2020) made a similar observation, reporting that plants cultivated in increased CO<sub>2</sub> had decreased nitrogen content, which led to an increase in the number of webblings per plant by *Maruca vitrata* (Fabricius) to compensate for their nutritional requirements, resulting in more webbing than plants grown in ambient CO<sub>2</sub> and temperature. This is consistent with the majority of prior research suggesting that insect larvae may devour up to 80% more leaves from plants cultivated under elevated CO<sub>2</sub> treatments (Fajer *et al.* 1989, Williams *et al.* 2003, Xie *et al.* 2015).

*Effect on growth and development of S. frugiperda larvae:* Larval weight also varies substantially across all treatments. The highest larval weight (592.0 ± 1.64 mg) was found in eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C and the lowest larval weight (523.0 ± 1.25 mg) was observed in a reference plot. The findings showed that *S. frugiperda* larvae gained higher weight and also lengthening its larval duration (28.3 ± 0.05 days) from the first (3.90 ± 0.04 days), second (4.18 ± 0.05 days), third (4.75 ± 0.03 days), fourth (4.88 ± 0.12 days), fifth (5.10 ± 0.09 days) and sixth instar (5.66 ± 0.04 days) under eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C. It is generally recognized that more food consumed by larvae results in increased weight gain. Moreover, physically debilitated fall armyworms feeding on low-quality hosts are more likely to delay their development. The current findings on larval weight and duration are in agreement with those of Stiling *et al.* (1999), Adati *et al.* (2004), Zvereva and Kozlov (2006) and Megha (2020). The findings showed that *S. frugiperda* larvae

Table 3 Effect of elevated CO<sub>2</sub> and temperature at the second trophic level (*S. frugiperda*)

Treatment details	Davis scale	Larval, pupal and adult parameters				
	Leaf area damage by <i>S. frugiperda</i> larvae (Score)	Larval weight of 6 <sup>th</sup> instar (mg)	Total larval period (days)	Pupal weight (mg)	Pupal duration (days)	Fecundity/ Female (Numbers)
aCO <sub>2</sub> @410 ppm + 31°C	4.53 <sup>d</sup>	553.5 ± 5.33 <sup>c</sup>	26.48±0.20 <sup>bc</sup>	217.6 ± 2.33 <sup>ab</sup>	13.68 ±0.40 <sup>bc</sup>	1010 (31.76) <sup>c</sup>
aCO <sub>2</sub> @410 ppm + 33°C	5.13 <sup>c</sup>	551.5 ± 3.23 <sup>c</sup>	25.88± 0.03 <sup>c</sup>	207.2 ± 2.98 <sup>b</sup>	14.30 ±0.20 <sup>b</sup>	1210 (34.76) <sup>b</sup>
eCO <sub>2</sub> @550 ppm + 31°C	5.63 <sup>b</sup>	574.7 ± 3.02 <sup>b</sup>	27.38± 0.25 <sup>ab</sup>	172.3 ± 1.15 <sup>d</sup>	16.75 ±0.31 <sup>a</sup>	720 (26.80) <sup>d</sup>
eCO <sub>2</sub> @550 ppm + 33°C	6.36 <sup>a</sup>	592.0 ± 1.64 <sup>a</sup>	28.03± 0.05 <sup>a</sup>	189.3 ± 1.44 <sup>c</sup>	16.37 ±0.40 <sup>a</sup>	730 (27.00) <sup>d</sup>
Reference plot	3.87 <sup>e</sup>	523.0 ± 1.25 <sup>d</sup>	24.20± 0.43 <sup>d</sup>	225.7 ± 6.37 <sup>a</sup>	13.25 ±0.28 <sup>c</sup>	1420 (37.68) <sup>a</sup>
CV (%)	2.39	1.3	1.81	3.8	1.71	3.8
SEM (±)	0.05	3.2	0.24	3.4	0.03	0.5
CD (p=0.01)	0.28	16.8	1.14	17.7	0.14	2.8

Means denoted by the same letters in the vertical column are not significantly different by DMRT; Mean ± SD are separated by the least significant difference; Figures in parentheses are arcsine transformed values.

gained more weight under eCO<sub>2</sub> conditions. It is generally recognized that more food consumed by larvae results in increased weight gain. These results are consistent with experimental evidence from Srinivasa *et al.* (2012) who showed that castor-fed larvae of *Achea janata* (Linnaeus) and *Spodoptera litura* (Fabricius) gained more weight under eCO<sub>2</sub> conditions than under aCO<sub>2</sub> conditions. The present results were also in agreement with Shwetha *et al.* (2019), who revealed that when larvae were fed groundnut foliage produced under eCO<sub>2</sub> conditions rather than aCO<sub>2</sub> settings, the weight of the larvae increased by 2.4%.

*Effect on pupal stage and fecundity of S. frugiperda:* The pupal duration was also recorded, highest pupal duration under eCO<sub>2</sub> at 550 ppm was reported at 16.75 ± 0.31 days while significantly least duration (13.25 ± 0.28 days) was recorded in reference plot. Meanwhile, maximum pupal weight was obtained in reference plot (225.7 ± 6.37 mg) and was considerably less in eCO<sub>2</sub> at 550 ppm (172.3 ± 1.15 mg). Female fecundity in the reference plot was much higher (1420/female), while the lowest fecundity was recorded by eCO<sub>2</sub> at 550 ppm (720/female) (Table 3). Compared with the ambient climatic conditions, the results demonstrated that the enhanced climate change treatments significantly decreased the fecundity of female moths. Meanwhile, the decrease in pupal weight and female fecundity may be due to malnutrition or weak adults by inadequate nutrition due to poor food quality during the larval period, which led to decreased pupal weights and the generation of weak adults in elevated conditions, which in turn led to a decrease in fecundity rate (Liu *et al.* 2017, Shwetha *et al.* 2019, Megha 2020).

#### *Effect of elevated temperature and CO<sub>2</sub> at the third trophic level*

*Parasitism rate of Trichogramma chilonis on S. frugiperda eggs:* At the tri-trophic level, *Trichogramma chilonis* plays an important role in dampening the fall armyworm pest populations. However, climate change may exacerbate pest problems by increasing herbivore performance and decreasing overall quality, while

concurrently decreasing top-down control by biological control agents. From the current investigation, highest parasitism rate (83.44%) and emergence rate (87.59%) were observed on the eggs of *S. frugiperda* under untreated open conditions, whereas the lowest parasitism rate (63.18%) and least emergence (61.93%) was observed in eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C. However, *T. chilonis* development time inside fall armyworm eggs was regulated by host quality, which was mediated by climatic change. The parasitoid provided by *S. frugiperda* eggs treated under eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C had the longest developmental period (11 days) (Table 4). The present investigation is supported by studies on other parasitoid species, which have shown similar results with decreased parasitism rates. These include the studies by Vuorinen *et al.* (2004), Chen *et al.* (2005), and Klaiber *et al.* (2013), who reported reduced parasitoid fitness, parasitism rate, and prolonged developmental time. Chen *et al.* (2007) reported that there was a significant decrease (10%) in the emergence rate of *Aphidius picipes* (Viereck) under 750 ml/L CO<sub>2</sub> compared to ambient CO<sub>2</sub>. Wang *et al.* (2014) reported that elevated CO<sub>2</sub> did not affect the developmental duration, parasitization rate, or adult emergence rate of *Encarsia formosa* (Gahan) after parasitizing *Bemisia tabaci* (Gennadius) for three successive generations. In contrast, Stiling *et al.* (1999) reported that the increased mortality of oak leaf miners was due to a higher attack rate by parasitoids, eliciting greater top-down pressure from natural enemies.

*Parasitism rate of G. nephantidis on S. frugiperda larvae:* *G. nephantidis* is a gregarious larval parasitoid responsible for the reduction in various pest populations under field conditions. Although its successful performance on fall armyworm is scanty, the results of the experiment indicated that it could serve as a potential biological control agent against fall armyworm. However, under the influence of high CO<sub>2</sub> at 550 ppm and temperature at 33°C, unfavourable findings such as lower body size, number of eggs deposited, and emergence rate were observed, reducing fitness and potential. It was observed that the maximum

Table 4 Effect of elevated CO<sub>2</sub> and temperature at the third trophic level (*T. chilonis*)

Treatment details	Percent parasitism of FAW eggs by <i>T. chilonis</i> (%)	Developmental period of <i>T. chilonis</i> (days)	Percent Emergence of <i>T. chilonis</i> (%)
aCO <sub>2</sub> @410 ppm + 31°C	78.71 (62.53) <sup>ab</sup>	8.75 ± 0.25 <sup>c</sup>	82.14 (65.01) <sup>bc</sup>
aCO <sub>2</sub> @ 410 ppm + 33°C	71.14 (57.54) <sup>bc</sup>	9.50 ± 0.25 <sup>bc</sup>	85.35 (67.51) <sup>ab</sup>
eCO <sub>2</sub> @550 ppm + 31°C	69.40 (56.46) <sup>c</sup>	10.25 ± 0.25 <sup>ab</sup>	77.98 (62.05) <sup>c</sup>
eCO <sub>2</sub> @550 ppm + 33°C	63.18 (52.64) <sup>c</sup>	11.00 ± 0 <sup>a</sup>	61.93 (51.91) <sup>d</sup>
Reference/Open plot	83.44 (66.33) <sup>a</sup>	8.50 ± 0.28 <sup>c</sup>	87.59 (69.46) <sup>a</sup>
CV (%)	4.93	4.87	2.73
SEM (±)	1.46	0.23	0.90
CD ( <i>p</i> =0.01)	7.00	1.11	4.27

Means denoted by the same letters in the vertical column are not significantly different by DMRT; Mean ± SD are separated by the least significant difference; Figures in parentheses are arcsine transformed values. FAW, Fall armyworm.

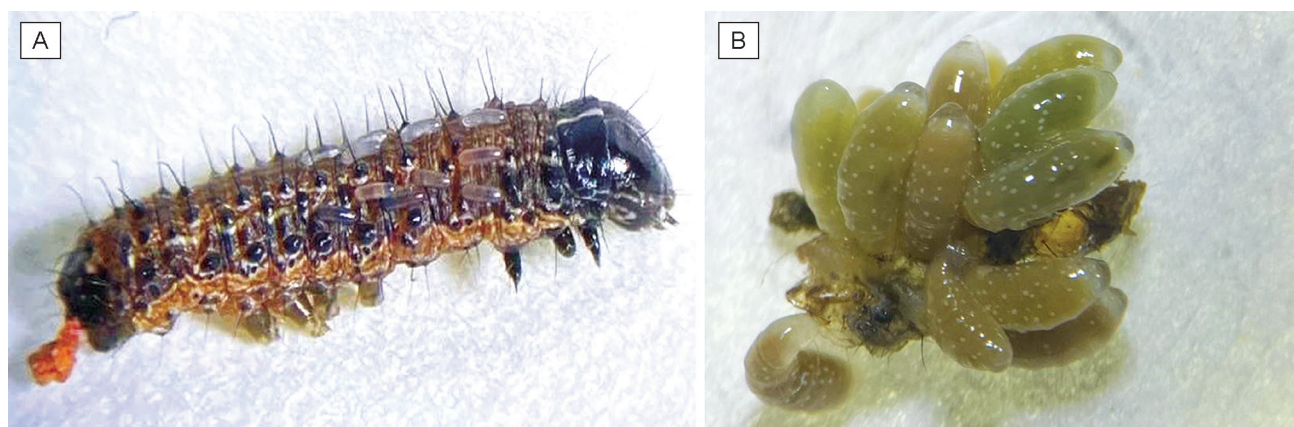


Fig. 1 (A) Eggs of *G. nephantidis* on *S. frugiperda*; (B) Grubs of *G. nephantidis* on *S. frugiperda*.

number of eggs of *G. nephantidis* were laid predominantly on the dorso-lateral side of the abdominal segments of *S. frugiperda* fourth instar larvae, but also on the thorax and the last segment of the abdomen. The egg was loosely attached to the integument of the host and deposited parallel to the longitudinal axis of the body (Fig. 1A), which later turned into grubs (Fig. 1B).

Maximum numbers of eggs were laid in controlled condition ( $19.91 \pm 0.19$  eggs/female) while the least number of eggs ( $12.60 \pm 0.56$  eggs/female) was laid under eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C condition while the incubation period did not vary significantly across the treatments. The number of grubs that emerged from the eggs was tallied, and was found to be lower under elevated CO<sub>2</sub> conditions. Maximum numbers of grubs was recorded by reference condition ( $19.10 \pm 0.31$  grubs). The number of cocoons that transformed from the grub without desiccation

was also tallied, while the maximum number of cocoons ( $18.35 \pm 0.28$ ) was found in the reference condition and least under eCO<sub>2</sub> at 550 ppm + raised temperature at 33°C ( $8.60 \pm 0.21$ ), while the maximum pupal weight was recorded under the reference condition ( $1.22 \pm 0.01$  mg). Highest number of emerged *G. nephantidis* adults was observed reference condition ( $17.78 \pm 0.02$ ) with highest per cent emergence under reference condition (89.32%) (Table 5). There are no reports of *G. nephantidis* under climate change conditions. However, the present investigation is supported by various studies that were recorded in natural enemy species other than *G. nephantidis*, viz. *Cotesia plutella* (Linnaeus) by Vuorinen *et al.* (2004), *Aphidius picipes* (Nees) by Chen *et al.* (2007), and *Diaretiella rapae* (MsIntosh) by Klaiber *et al.* (2013). However, Yin *et al.* (2009) reported that the rates of parasitism, cocooning, emergence, weight, and adult lifespan by *Microplitis mediator* (Haliday) in

Table 5 Effect of elevated CO<sub>2</sub> and temperature at the third trophic level (*G. nephantidis*)

Treatment details	Growth performance of <i>Goniozus nephantidis</i>						Morphometrics of <i>Goniozus nephantidis</i>			
	Number of eggs/female	Number of grubs	Number of pupae	Weight of pupae (mg)	No. of adult emerged	Adult emergence (%)	Size of egg (mm)	Size of grub (mm)	Size of cocoon (mm)	Size of adult (mm)
aCO <sub>2</sub> @410 ppm + 31°C	17.90 ± 0.23 <sup>b</sup>	16.18 ± 0.19 <sup>c</sup>	15.50 ± 0.17 <sup>c</sup>	1.15 ± 0.01 <sup>b</sup>	15.15 ± 0.26 <sup>b</sup>	84.64 (66.99) <sup>ab</sup>	0.551 ± 0.005 <sup>a</sup>	4.26 ± 0.05 <sup>a</sup>	4.42 ± 0.07 <sup>b</sup>	4.04 ± 0.07 <sup>a</sup>
aCO <sub>2</sub> @410 ppm + 33°C	17.60 ± 0.25 <sup>b</sup>	17.70 ± 0.35 <sup>b</sup>	16.65 ± 0.23 <sup>b</sup>	1.109 ± 0.02 <sup>b</sup>	14.08 ± 0.25 <sup>b</sup>	79.97 (63.47) <sup>b</sup>	0.542 ± 0.004 <sup>a</sup>	4.16 ± 0.03 <sup>ab</sup>	4.36 ± 0.07 <sup>b</sup>	3.82 ± 0.06 <sup>ab</sup>
eCO <sub>2</sub> @550 ppm + 31°C	14.10 ± 0.28 <sup>c</sup>	10.85 ± 0.26 <sup>d</sup>	9.90 ± 0.42 <sup>d</sup>	1.03 ± 0.02 <sup>c</sup>	9.25 ± 0.57 <sup>c</sup>	65.60 (54.26) <sup>c</sup>	0.536 ± 0.003 <sup>a</sup>	4.02 ± 0.01 <sup>ab</sup>	3.93 ± 0.07 <sup>c</sup>	3.68 ± 0.08 <sup>bc</sup>
eCO <sub>2</sub> @550 ppm + 33°C	12.60 ± 0.56 <sup>d</sup>	10.10 ± 0.31 <sup>d</sup>	8.60 ± 0.21 <sup>c</sup>	0.97 ± 0.01 <sup>c</sup>	8.33 ± 0.09 <sup>c</sup>	66.07 (54.65) <sup>c</sup>	0.542 ± 0.007 <sup>a</sup>	3.85 ± 0.09 <sup>b</sup>	3.82 ± 0.05 <sup>c</sup>	3.50 ± 0.02 <sup>c</sup>
Reference/Open plot	19.90 ± 0.19 <sup>a</sup>	19.10 ± 0.31 <sup>a</sup>	18.35 ± 0.28 <sup>a</sup>	1.22 ± 0.01 <sup>a</sup>	17.78 ± 0.02 <sup>a</sup>	89.32 (71.01) <sup>a</sup>	0.557 ± 0.004 <sup>a</sup>	4.39 ± 0.01 <sup>a</sup>	4.75 ± 0.06 <sup>a</sup>	4.12 ± 0.09 <sup>a</sup>
CV (%)	4.06	3.94	4.05	4.70	4.93	4.21	1.95	4.74	3.68	4.21
SEM (±)	0.33	0.29	0.28	0.01	0.32	1.31	0.004	0.08	0.07	0.07
CD (p=0.01)	1.02	0.89	0.85	0.04	0.98	6.27	0.02	0.26	0.36	0.37

Means denoted by the same letters in the vertical column are not significantly different by DMRT; Mean ± SD are separated by the least significant difference; Figures in parentheses are arcsine transformed values.

*Helicoverpa armigera* (Hubner) were unaffected. Apart from hymenopterans, Holton *et al.* (2003) reported that the dipteran parasitoid *Compsilura concinnata* (Meigen) decreased under elevated CO<sub>2</sub>.

*Morphometric measurement of G. nephantidis mediated by larvae S. frugiperda*: The data on morphometry of egg showed that length of the eggs varied from 0.53–0.56 mm in length across the treatments but there was non-significant difference across the treatments. However, length of the grub (4.39 ± 0.01 mm), length of the cocoon (4.75 ± 0.06 mm), and length of the adult female (4.12 ± 0.09 mm) were maximum under the reference condition (Table 5). The decrease in the *G. nephantidis* indicated a negative impact caused by elevated CO<sub>2</sub> and temperature conditions. However, there have been no earlier reports on morphometry for comparison with the present investigations. However, studies on duration and parasitism are well supported by various authors, who have reported similar results (Vuorinen *et al.* 2004).

In conclusion, climate change, whether in terms of elevated CO<sub>2</sub> alone or in combination with increased temperature, has supported the growth, development, and yield of maize, indicating that mono-trophic interactions favour the crop. However, when considering climate change at the bi-trophic level, particularly the impact on fall armyworm, a more negative influence was observed. This leads to increased damage to the crop, alterations in larval duration, decreased fecundity of females, and a reduction in overall fitness. Furthermore, climate change at the tri-trophic level, affecting parasitoids, also exhibited negative effects, such as decreased parasitism rate, emergence rate, and reduction in size as a result of the declining quality of their host. Therefore, we speculate that increased temperature and CO<sub>2</sub> concentrations could exacerbate the negative effects on tri-trophic interactions in maize ecosystem.

#### REFERENCES

- Adati T, Satoshi N, Tamo M and Kawazu K. 2004. Effect of temperature on development and survival of legume pod borer *Maruca vitrata* (Fabricius) (Lepidoptera: Pyralidae) reared on a semi synthetic diet. *Applied Entomology and Zoology* **39**(1): 139–45.
- Adishesha K, Janagoudar B S, Amaregouda A, Shanawad U K and Chandranaik M. 2017. Morphological charaters of maize (*Zea mays* L.) genotypes to elevated carbon dioxide and temperature regimes. *Indian Journal of Pure and Applied Biosciences* **5**(5): 163–70.
- Anonymous. 2021. *Package of Practice*. University of Agricultural Sciences, Raichur, Karnataka, pp. 53–55.
- Berliner E. 1915. Ueber die schlafsucht der *Ephestia kuhniella* und *Bac. thuringiensis* n. sp. *Zeitschrift für angewandte Entomologie* **2**: 21–56.
- Berryman A A. 1996. What causes population cycles of forest Lepidoptera? *Trends in Ecology and Evolution* **11**(1): 28–32.
- Chen F J, Wu G, Parajulee M N and Ge F. 2007. Impact of elevated CO<sub>2</sub> on the third trophic level: A predator *Harmonia axyridis* and a parasitoid *Aphidius picipes*. *Biocontrol Science and Technology* **17**(3): 313–24.
- Chen F, Ge F and Parajulee M N. 2005. Impact of elevated CO<sub>2</sub> on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Leis axyridis*. *Environmental Entomology* **34**(1): 37–46.
- Chormule A, Shejawal N, Sharanabasappa C M, Asokan R, Swamy H M and Studies Z. 2019. First report of the fall armyworm, *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae) on sugarcane and other crops from Maharashtra, India. *Journal of Entomology and Zoology Studies* **7**(1): 114–17.
- Dash C K, Bamisile B S, Mitra S, Qasim M, Hussain M, Hmeed M S and Wang L. 2017. Impacts of climate change on plant-herbivore-natural enemy interactions. *Journal of Biology, Agriculture and Healthcare* **7**(16): 18–24.
- Dyer L A, Richards L A, Short S A and Dodson C D. 2013. Effects of CO<sub>2</sub> and temperature on tritrophic interactions. *PLOS One* **8**(4): 62528.
- Fajer E D, Bowers M D and Bazzaz F A. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Journal of Insect Behaviour* **243**(4895): 1198–200.
- Gray S B and Brady S M. 2016. Plant developmental responses to climate change. *Developmental Biology* **419**(1): 64–77.
- Guyer A, van Doan C, Maurer C, Machado R A, Mateo P, Steinauer K, Kesner L, Hoch G, Kahmen A, Erb M and Robert C A. 2021. Climate change modulates multitrophic interactions between maize, a root herbivore, and its enemies. *Journal of Chemical Ecology* **47**(10): 889–906.
- Holton M K, Lindroth R L and Nordheim E V. 2003. Foliar quality influences tree-herbivore-parasitoid interactions: Effects of elevated CO<sub>2</sub>, O<sub>3</sub>, and plant genotype. *Oecologia* **137**: 233–44.
- Intergovernmental Panel on Climate Change. 2022. Climate Change 2022: Impacts, Adaptation and Vulnerability. (In) *12<sup>th</sup> Session of Working Group II and 55<sup>th</sup> Session of the IPCC*. <https://www.ipcc.ch/report/sixth-assessment-report-working-group-ii/>
- Klaiber J, Najar-Rodriguez A J, Dialer E and Dorn S. 2013. Elevated carbon dioxide impairs the performance of a specialized parasitoid of an aphid host feeding on *Brassica* plants. *Biological Control* **66**(1): 49–55.
- Liu J, Haung W, Chi H, Wang C, Hua H and Wu G. 2017. Effects of elevated CO<sub>2</sub> on the fitness and potential damage of *Helicoverpa armigera* based on two-sex life table. *Scientific Reports* **7**: 1119.
- Megha. 2020. 'Effect of climate change on growth and development of cowpea pod borer, *Maruca vitrata* (Fabricius) and aphid, *Aphis craccivora* (Koch) mediated by Cowpea'. MSc Thesis, University of Agricultural Sciences, Raichur, Karnataka.
- Miri H R, Rastegar A and Bagheri A R. 2012. The impact of elevated CO<sub>2</sub> on growth and competitiveness of C<sub>3</sub> and C<sub>4</sub> crops and weeds. *European Journal of Experimental Biology* **2**(4): 1144–50.
- Montezano D G, Sosa-Gomez D R, Specht A, Roque-Specht V F, Sousa-Silva J C, Paula-Moraes S D, Peterson J A and Hunt T E. 2018. Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *African Entomology* **26**(2): 286–300.
- Mounica D, Krishnayya P V and Patibanda A K. 2020. Interactive effect of elevated CO<sub>2</sub> and temperature on the biochemical constituents of maize, *Zea mays* (L.) and its impact on the fecundity of maize aphid, *Rhopalosiphum maidis* (F.). *Journal of Pharmacognosy and Phytochemistry* **9**(6): 1005–10.
- Moya T B, Ziska L H, Namuco O S and Olszyk D. 1998. Growth dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide

- and temperature. *Global Change Biology* **4**(6): 645–56.
- Pooja D. 2022. 'Effect of climate change on fall armyworm, *Spodoptera frugiperda* (J. E. Smith) mediated by Maize'. MSc Thesis, University of Agricultural Sciences, Raichur, Karnataka.
- Reich P B, Hungate B A and Luo Y. 2006. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution, and Systematics* **37**(1): 611–36.
- Robinson E A, Ryan G D and Newman J A. 2012. A meta-analytical review of the effects of elevated CO<sub>2</sub> on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist* **194**(2): 321–36.
- Sari J H, Nissinen A, Dong W X, Neal S C, Stewart Jr C N, Poppy G M and Holopainen J K. 2008. Interactions of elevated carbon dioxide and temperature with aphid feeding on transgenic oilseed rape: Are *Bacillus thuringiensis* (*Bt*) plants more susceptible to non-target herbivores in future climate? *Global Change Biology* **14**(6): 1437–54.
- Shwetha, Sreenivas A G, Ashoka J, Nadagoud S and Kuchnoor P H. 2019. Effect of elevated CO<sub>2</sub> and temperature on biochemistry of groundnut and in turn its effect on development of leaf eating caterpillar, *Spodoptera litura* Fabricius. *Legume Research* **42**(3): 399–404.
- Srinivasa Rao M, Manimanjari D, Vanaja M, Rama Rao C A, Srinivas K, Rao V U M, Venkateswarlu B and Jay R. 2012. Impact of elevated CO<sub>2</sub> on tobacco caterpillar, *Spodoptera litura* on peanut, *Arachis hypogea*. *Journal of Insect Science* **12**(1).
- Stiling P, Rossi A M, Hungate B, Dijkstra P, Hinkle C R, Knott III W M and Drake B. 1999. Decreased leaf-miner abundance in elevated CO<sub>2</sub>: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* **9**(1): 240–44.
- Sun Y C, Feng L, Gao F and Ge F. 2011a. Effects of elevated CO<sub>2</sub> and plant genotype on interactions among cotton, aphids and parasitoids. *Insect Science* **18**(4): 451–61.
- Sun Y C, Yin J, Chen F J, Wu G and Ge F. 2011b. How does atmospheric elevated CO<sub>2</sub> affect crop pests and their natural enemies? Case histories from China. *Insect Science* **18**(4): 393–400.
- Tefera T, Gofitshu M, Ba M N and Muniappan R M. 2019. *A Guide to Biological Control of Fall Armyworm in Africa Using Egg Parasitoids*, 1<sup>st</sup> edn. Nairobi, Kenya.
- Vuorinen T, Nerg A M, Ibrahim M A, Reddy G V P and Holopainen J K. 2004. Emission of *Plutella xylostella*-induced compounds from cabbages grown at elevated CO<sub>2</sub> and orientation behaviour of the natural enemies. *Plant Physiology* **135**(4): 1984–92.
- Wang G H, Wang X X, Sun Y C and Ge F. 2014. Impacts of elevated CO<sub>2</sub> on *Bemisia tabaci* infesting *Bt* cotton and its parasitoid *Encarsia formosa*. *Entomologia Experimentalis et Applicata* **152**(3): 228–37.
- Williams R S, Lincoln D E and Norby R J. 2003. Development of gypsy moth larvae feeding on red maple saplings at elevated CO<sub>2</sub> and temperature. *Oecologia* **137**: 14–122.
- Xie H, Zhao L, Yang Q, Wang Z and He K. 2015. Direct effects of elevated CO<sub>2</sub> levels on the fitness performance of Asian corn borer (Lepidoptera: Crambidae) for multigenerations. *Environmental Entomology* **44**(4): 1250–57.
- Yin J, Sun Y, Wu G, Parajulee M N and Ge F. 2009. No effects of elevated CO<sub>2</sub> on the population relationship between cotton bollworm, *Helicoverpa armigera* Hubner (Lepidoptera: Noctuidae), and its parasitoid, *Microplitis mediator* Haliday (Hymenoptera: Braconidae). *Agriculture, Ecosystems and Environment* **132**(3–4): 267–75.
- Zvereva E L and Kozlov M V. 2006. Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: A metaanalysis. *Global Change Biology* **12**(1): 27–41.